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Beta-Diversity Patterns and Community Assembly across Latitudes

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Beta-Diversity Patterns and Community Assembly across Latitudes
by
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A dissertation presented to
The Graduate School
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

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List of Abbreviations

SAD – species abundance distribution; the distribution of each species' abundance in a community or region

PIE – probability of interspecific encounter; an evenness metric that measures the probability of encountering a different species given a random sampling of an individual from the same species abundance distribution

PCA – principal components analysis; statistical procedure that transforms multiple variables into a set of uncorrelated variables termed principal components

PCR – principal components regression; statistical analysis that uses principal components as the predictor variables in a multiple regression

α -diversity – local diversity; general term for the quantification of evenness of the species abundance distribution in a single community

β -diversity – turnover; general term for a group of metrics that quantify variation in species composition in space or time

γ -diversity – regional diversity; general term for the quantification of evenness of the species abundance distribution across a group of local communities; calculated like local diversity after grouping all individuals encountered in local communities into a single larger "region."

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Abstract

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A major goal of community ecology is in understanding variation in community composition, generally termed β -diversity. This variation can result from a variety of mechanisms, including deterministic factors, wherein species sort along biotic or abiotic gradients; stochastic processes, whereby random fluctuations in population sizes cause variation in community composition; and/or dispersal limitation. Although all of these processes are likely occurring in all biological communities, a key question in community ecology research is if their relative importance may vary systematically across environmental or biogeographic gradients.

In this dissertation, we combine both observational and experimental research to investigate β -diversity across a biogeographic gradient of longstanding interest in ecology and evolutionary biology, the latitudinal gradient. Diversity at the local and/or regional scale has long been known to decrease with latitude, but only relatively recently have similar trends been shown for β -diversity as well. Although this may

suggest that community assembly processes that generate β -diversity may also be varying with latitude, β -diversity metrics are numerically dependent to varying degrees on different aspects of regional and local diversity. Therefore, any trends in β -diversity with latitude could simply be reflecting the well-documented trends in local and/or regional diversity, generally referred to as sampling effects. Throughout this dissertation, therefore, we employ a relatively uncommon β -diversity metric, heretofore termed β -pie, that is relatively insensitive to sampling effort (the number of individuals sampled locally) and to the shape of the regional species abundance distribution, which we believe will improve the assessment of how and why community composition may vary in space and time.

In Chapter 2, we apply this metric to zooplankton communities sampled across ten latitudes in North America and three years to determine if, after accounting for the aforementioned sampling effects, there are any general trends of spatial and/or temporal turnover with latitude. Although we recovered a significant relationship between spatial β -pie and latitude in two years, these trends actually reversed from one year to the next, and there was no significant relationship in the third year. Unlike other studies documenting temporal turnover as a function of latitude, we found no relationship between temporal β -pie and latitude. These results together suggest that systematic variation in β -diversity along local and/or regional diversity gradients (such as with latitude) may simply be reflecting numerical sampling effects instead of systematic variation in community assembly processes.

Chapters 3 and 4 report the results of large-scale outdoor mesocosm experiments replicated at three latitudes in North America. By using mesocosms, we

attempted to limit abiotic heterogeneity and historical differences, but allow for natural variation in regional species pools to affect community assembly. Chapter 3 specifically focuses on the role of an environmental filter, drought, and asks how it affects within-site aggregation, as well as whether its effect on β -pie varies consistently with latitude. Interestingly, we found that β -pie could either increase or decrease after the drought treatment, and although we did find regional differences in its effect, these did not vary systematically with latitude. In addition, it appears that variation in β -pie was not due to changes in local diversity (α -pie) but largely caused by changes in the regional species abundance distribution (γ -pie).

Chapter 4 focused on how dispersal at different stages of assembly affects β -pie. Because we did not intentionally impose abiotic heterogeneity, this experiment focused on the interaction between dispersal, stochasticity, and species interactions in generating intraspecific aggregation during community assembly. The two dispersal treatments occurred at different stages of assembly – 1) during the initial establishment of communities, when population sizes are relatively small and demographic stochasticity might generate high variation in initial colonists, and 2) two years after communities have assembled, when population sizes are much larger and species have a greater potential to deterministically interact. Like the drought treatment, we found variable effects of dispersal on β -pie. The early dispersal treatments (high versus low) were found to increase, decrease, or have no effect on aggregation, and there was no general trend with latitude. The late dispersal treatment effects did show some interesting trends for passive dispersers, however, wherein the high dispersal treatment actually increased β -pie relative to the controls. In addition, this effect tended to

decrease with latitude, suggesting that perhaps dispersal limitation plays a greater role in community assembly with decreasing latitude.

Chapter 1: Introduction

In 1975 Jared Diamond proposed that communities assemble according to certain ecological rules. These “assembly rules” were based on decades of observational work on island bird communities and aimed to explain why different communities exist and persist in similar abiotic environments. The emphasis of Diamond’s assembly rules was on biotic interactions, mainly competition, which prohibited the co-occurrence of certain species combinations. Further, these communities were relatively stable through time, meaning that potential invaders were prohibited from entering a community if the resident species were not “compatible.” In other words, earlier dispersers had priority over later ones. Although community ecology has largely moved away from Diamond’s assembly rules, per se, the field still widely embraces the roles of deterministic species interactions, dispersal, and priority, or historical contingency, in trying to understand why communities vary in space and time (Fukami 2015).

The disfavor of assembly rules began shortly after their proposal due to a seminal paper by Connor and Simberloff (1979), which challenged the need for species interactions to create a patchy compositional landscape. Instead, they proposed that chance dispersal events alone could result in the same patterns of species compositional variation among islands. These ideas were later expanded by Hubbell’s unified neutral theory of biodiversity (2001), which could also recreate ecological patterns, such as species area relationships and species abundance distributions (Bell 2000, Hubbell 2001), very similar to those observed in nature with just three

mechanisms - speciation, dispersal, and ecological drift. Notably, species traits, species interactions, or the suitability of the abiotic environment, which are the basis of niche theory and arguably most of ecology, were entirely left out.

Currently, community ecology embraces aspects of all of these ideas.

Metacommunity theory has been a particularly useful framework that integrates deterministic and stochastic elements of community assembly to better understand how communities form and change through space and time, generally termed β -diversity (Whittaker 1960, Whittaker 1972, Leibold et al. 2004). There are four general metacommunity paradigms – species sorting, patch dynamics, mass effects, and neutral - that emphasize to varying degrees the importance of the biotic and abiotic environment, dispersal, and stochasticity and historical contingency. Although it is unlikely these exact types of metacommunities are represented in nature, a key interest in community ecology today is in trying to understand when these processes may vary in their relative importance (Ricklefs and Schluter 1993, Chase and Myers 2011, Fukami 2015).

Of longstanding interest in ecology and evolutionary biology is how ecological processes may differentially influence species and communities with latitude. For example, many have suggested that the species-rich, low latitude communities are highly regulated by strong biotic interactions, while the harsh and variable abiotic environment plays a greater role in high latitude communities (Schemske et al. 2009). Interestingly, there is also increasing evidence for a latitudinal gradient in β -diversity (e.g. Koleff et al. 2003, Soininen et al. 2007), and some emerging work is investigating if variation in β -diversity with latitude indicates variation in community assembly

mechanisms. For example, Myers et al. (2013) found that the proportion of variance in community composition (β -diversity) explained by space (as a proxy for dispersal limitation) and the abiotic environment varied between tropical and temperate forests, while Freestone and Inouye (2015) found that the spatial and temporal β -diversity of sessile marine invertebrate communities appeared more stochastically assembled in temperate versus tropical zones.

In recent decades, however, the quantification and interpretation of β -diversity has been greatly debated (Jost 2007, Tuomisto 2010a, Tuomisto 2010b). Of primary importance in these debates is the degree to which a given β -diversity metric is dependent on local (α -) and/or regional (γ -) diversity, and if comparisons of β -diversity among regions are ecologically meaningful (Jost 2007, Anderson et al. 2011). There are both additive ($\beta = \gamma - \alpha$) and multiplicative ($\beta = \gamma/\alpha$) β -diversity metrics, but the nature of these equations, and the scaling of diversity, makes it impossible for all three parameters to be simultaneously independent (Ricotta 2010). As it is well documented that local and regional diversity decrease with latitude, it is therefore difficult to assess if latitudinal variation in β -diversity reflects variation in community assembly processes, or if it simply reflects changes in local and/or regional diversity (i.e. numerical sampling effects).

A common way that researchers have addressed this interdependence of α -, β -, and γ -diversity is through the use of null modeling (Chase et al. 2011, e.g. Kraft et al. 2011, Stegen et al. 2013, Qian and Wang 2015). Although null models vary in their assumptions, a general approach is to take observed aspects of the regional species pool and randomly assign either species or individuals to local communities. β -diversity

can be calculated for these simulated communities and compared to observed β -diversity values to assess the degree to which regional and/or local constraints could be responsible for generating the observed β -diversity values. These null models are also often used as null hypotheses to interpret community assembly processes, specifically to distinguish purely stochastic assembly, from non-stochastic, deterministic assembly (e.g. Chase 2003, 2007, Chase 2010, Kraft et al. 2011, De Caceres et al. 2012, Stegen et al. 2013, Tucker et al. 2016). However, it is becoming increasingly apparent that capturing assembly mechanisms using such null models is highly contingent on the β -diversity metric used, the method of the simulations themselves, and the ways in which stochastic and deterministic processes are affecting community composition (Vellend et al. 2014, Mori et al. 2015, Xu et al. 2015, Tucker et al. 2016).

In this doctoral dissertation, we investigated community assembly across latitudes, using an uncommonly employed metric of β -diversity, here termed β -pie. β -pie is relatively insensitive to sampling effort (community size/number of individuals sampled in local communities) or to the size or shape of the regional species pool, and thus does not require the employment of null models. Instead, β -pie values only deviate from zero when there is significant intraspecific aggregation (in space or time) that does not reflect numerical sampling effects of varying local or regional diversity. Conversely, as β -pie approaches zero, intraspecific aggregation approaches that which could be expected given stochastic assembly from the regional species pool.

In chapter 1, we explored β -diversity of freshwater zooplankton communities across latitudes in North America. This was done for three consecutive years, and for multiple ponds per region, allowing for the quantification of both spatial and temporal β -

pie. Curve fitting between β -pie and latitude was performed to assess if there are any general trends in turnover after accounting for numerical sampling effects. Chapters 2 and 3 present the results of large-scale outdoor mesocosm experiments replicated at three latitudes in North America. Employing experiments allowed us to largely control for variation in the abiotic environment and history, to more easily quantify the effects of specific assembly processes on community composition. The first experiment investigated the effect of an environmental filter, drought, while the second experiment manipulated dispersal to assess if stochasticity in colonization and variation in the biotic environment may interact to differentially affect community assembly across latitudes.

1.1 References

- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters* **14**:19-28.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* **155**:606-617.
- Chase, J. M. 2003. Community assembly: when should history matter? *Oecologia* **136**:489-498.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* **104**:17430-17434.
- Chase, J. M. 2010. Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science* **328**:1388-1391.
- Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. C. a. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere* **2**:1-11.
- Chase, J. M. and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **366**:2351-2363.

- Connor, E. F. and D. Simberloff. 1979. The Assembly of Species Communities - Chance or Competition. *Ecology* **60**:1132-1140.
- De Caceres, M., P. Legendre, R. Valencia, M. Cao, L. W. Chang, G. Chuyong, R. Condit, Z. Q. Hao, C. F. Hsieh, S. Hubbell, D. Kenfack, K. P. Ma, X. C. Mi, M. N. S. Noor, A. R. Kassim, H. B. Ren, S. H. Su, I. F. Sun, D. Thomas, W. H. Ye, and F. L. He. 2012. The variation of tree beta diversity across a global network of forest plots. *Global Ecology and Biogeography* **21**:1191-1202.
- Diamond, J. M. 1975. Assembly of species communities. Pages 342-444 *in* M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press
- Harvard University Press, Cambridge.
- Freestone, A. L. and B. D. Inouye. 2015. Nonrandom community assembly and high temporal turnover promote regional coexistence in tropics but not temperate zone. *Ecology* **96**:264-273.
- Fukami, T. 2015. Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. *Annual Review of Ecology, Evolution, and Systematics* **46**:1-23.
- Hubbell, S. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton, NJ.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* **88**:2427-2439.
- Koleff, P., J. J. Lennon, and K. J. Gaston. 2003. Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* **12**:483-498.

- Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science* **333**:1755-1758.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**:601-613.
- Mori, A. S., S. Fujii, R. Kitagawa, and D. Koide. 2015. Null model approaches to evaluating the relative role of different assembly processes in shaping ecological communities. *Oecologia* **178**:261-273.
- Myers, J. A., J. M. Chase, I. Jimenez, P. M. Jorgensen, A. Araujo-Murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters* **16**:151-157.
- Qian, H. and X. L. Wang. 2015. Global relationships between beta diversity and latitude after accounting for regional diversity. *Ecological Informatics* **25**:10-13.
- Ricklefs, R. E. and D. Schluter. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.
- Ricotta, C. 2010. On beta diversity decomposition: Trouble shared is not trouble halved. *Ecology* **91**:1981-1983.

- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is There a Latitudinal Gradient in the Importance of Biotic Interactions? *Annual Review of Ecology, Evolution, and Systematics* **40**:245-269.
- Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. *Ecography* **30**:3-12.
- Stegen, J. C., A. L. Freestone, T. O. Crist, M. J. Anderson, J. M. Chase, L. S. Comita, H. V. Cornell, K. F. Davies, S. P. Harrison, A. H. Hurlbert, B. D. Inouye, N. J. B. Kraft, J. A. Myers, N. J. Sanders, N. G. Swenson, and M. Vellend. 2013. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. *Global Ecology and Biogeography* **22**:202-212.
- Tucker, C. M., L. G. Shoemaker, K. F. Davies, D. R. Nemergut, and B. A. Melbourne. 2016. Differentiating between niche and neutral assembly in metacommunities using null models of beta-diversity. *Oikos* **125**:778-789.
- Tuomisto, H. 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* **33**:2-22.
- Tuomisto, H. 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* **33**:23-45.
- Vellend, M., D. S. Srivastava, K. M. Anderson, C. D. Brown, J. E. Jankowski, E. J. Kleynhans, N. J. B. Kraft, A. D. Letaw, A. A. M. Macdonald, J. E. Maclean, I. H. Myers-Smith, A. R. Norris, and X. X. Xue. 2014. Assessing the relative

- importance of neutral stochasticity in ecological communities. *Oikos* **123**:1420-1430.
- Whittaker, R. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**:279-338.
- Whittaker, R. J. 1972. Evolution and measurement of species diversity. *Taxon* **21**:213-225.
- Xu, W. B., G. K. Chen, C. R. Liu, and K. P. Ma. 2015. Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Global Ecology and Biogeography* **24**:1170-1180.

Chapter 2: Spatial and temporal turnover across latitudes

2.1 Introduction

Historically, ecologists viewed variation in the composition of species among localities, known as spatial β -diversity, primarily as the result of deterministic processes, whereby environmental factors and species interactions influence species composition (e.g. Whittaker 1967). More recently, the importance of stochasticity has been emphasized in the concept of ecological drift, in which random extinction and colonization events create compositional differences among communities (Hubbell 2001). An emerging synthesis is that both deterministic and stochastic processes operate simultaneously to create patterns of β -diversity, and a key goal is to discern whether there is any systematic variation in the relative importance of these processes across environmental and/or biogeographic gradients (Chase and Myers 2011, Vellend et al. 2014, Fukami 2015).

Variation in the relative importance of determinism and stochasticity in the assembly of communities may, in part, explain why there are gradients in the magnitude of spatial β -diversity, such as its systematic increase towards the tropics (Koleff et al. 2003b, Davidar et al. 2007, Qian et al. 2007, Qian and Ricklefs 2007, Soininen et al. 2007, Dahl et al. 2009, Kraft et al. 2011). As β -diversity is often related to environmental variation (Condit et al. 2002, Tuomisto et al. 2003, Qian and Ricklefs 2007), one potential explanation for this pattern is that environmental heterogeneity and/or the importance of environmental determinism decreases with latitude.

Alternatively, this same pattern can result from ecological drift or from simply stochastic sampling effects due to changing local or regional diversity. It is well documented that regional diversity increases towards the tropics, and thus, such sampling effects may cause greater spatial β -diversity with decreasing latitude (Chase and Myers 2011). Indeed, some recent studies (Kraft et al. 2011, De Caceres et al. 2012, Mori et al. 2015) show that stochastic sampling from regional species pools can account for much of the latitudinal variation in the spatial β -diversity (but see Qian and Wang 2015).

One limitation of most community assembly research is that tends to focus on static patterns of spatial β -diversity, even though assembly processes, such as dispersal or species interactions, are inherently dynamic and stochastic. For example, priority effects occur when early colonists deterministically prevent later ones from establishing in a local community. The identity of early colonists can stochastically vary among localities, such that priority effects result in alternative communities (spatial β -diversity) within the same region. Spatial β -diversity generated via priority effects, however, is difficult to distinguish from ecological drift using spatial data alone (Chase 2003, Fukami 2015). A key difference between priority effects and ecological drift is temporal stability in community membership; priority effects result in alternative stable communities that are expected to vary little through time, while ecological drift is expected to result in temporally varying communities (Chase 2010). Therefore, incorporating temporal data, measured as temporal β -diversity, along with spatial data, could aide in understanding community assembly processes and if they vary among regions. Nevertheless, the majority of community assembly research only considers the spatial component at snapshots in time (Micheli et al. 1999).

Further complicating the interpretation of β -diversity variation is the numerous ways researchers quantify β -diversity. For example, the slope of the species-area curve is often considered a measure of β -diversity, while pairwise metrics, such as the abundance-based Bray Curtis index or the presence-absence Jaccard's index, are very widely used (Koleff et al. 2003a, Tuomisto 2010, Anderson et al. 2011). Of major importance and intense debate in how to quantify β -diversity is that different metrics emphasize different aspects of variation in community composition and most metrics cannot separate, or make β -diversity independent from local (α) and/or regional (γ) diversity (Jost 2006, 2007, Jurasinski et al. 2009, Ricotta 2010, Tuomisto 2010, Anderson et al. 2011). Included in this debate are the effects of variations in sampling effort, or the number of individuals encountered, and the shape of the species abundance distribution (SAD), on β -diversity. This is problematic because the interpretation of β -diversity may not indicate anything about community assembly mechanisms, but simply reflect numerical sampling effects due to changes in local or regional abundances or SAD's (Chase and Knight 2013, Xu et al. 2015, Tucker et al. 2016).

In fact, the interdependence of α -, β -, and γ -diversity has long been discussed in community ecology, and a common way that researchers have attempted to correct for this is through the use of null models (e.g. Raup and Crick 1979, Chase 2007, Vellend et al. 2007, Chase 2010, Kraft et al. 2011, Myers et al. 2013). However, just as there are many ways to quantify β -diversity, there are also many ways to perform null models, each of which varies in which numerical aspects of α -, β -, and γ -diversity dependence they attempt to control. Complicating this even more is the fact that often

the goal of such null modeling is not just to correct for sampling effects, but also to act as a null hypothesis about community assembly mechanisms. In a recent paper by Mori et al. (2015), for example, the researchers investigated four types of null models: individual-based, species-based, probability-based, and richness-based. They additionally compared four different ways in which to actually quantify β -diversity, all of which were pairwise metrics. Although performance for their purposes varied with null model type and β -diversity metric, one of the paper's main conclusions was that simulating communities based on the number of individuals observed in local communities and the observed regional species pool performed the worst across all four β -diversity metrics. This is of note because this type of individual-based null model is very commonly used in community assembly research, such as in the high profile Kraft et al. paper (2011).

In this study, we use a less commonly used β -diversity metric (β -pie), that is relatively insensitive to changes in local abundances and regional SAD, to quantify both spatial and temporal β -diversity across a latitudinal gradient of ten sites in North America. The observational approach of this research allows us to investigate natural, rather than artificial, systems, and the quantification of both spatial and temporal turnover allows us to capture a more dynamic view of how communities assemble. Although several observational studies have shown that spatial β -diversity can vary with latitude (Harrison et al. 1992, Condit et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Beisner et al. 2006), fewer studies attempt to account for the numerical dependence of α -, β -, and γ -diversity through the use of null models (but see, e.g. Kraft et al. 2011, De Cáceres et al. 2012), and none to our knowledge have

used the aforementioned β -pie metric. Further, while some studies have investigated temporal β -diversity across latitudes (Shurin et al. 2007, Korhonen et al. 2010), these did not attempt to account for potential sampling effects of varying α - and γ -diversity with latitude. Finally, there have been some simultaneous investigations of spatial and temporal turnover (Adler and Lauenroth 2003, Adler et al. 2005), though we only know of one (Stegen et al. 2013) that takes a macroecological community assembly perspective.

In addition to examining community turnover as it relates to latitude, we further consider how some environmental factors may also relate to β -diversity. Importantly, these include variables such as nutrient concentrations as proxies for primary productivity, which has often been found to influence both spatial and temporal turnover in community composition (Chalcraft et al. 2004, Steiner and Leibold 2004, Gaston et al. 2007, Evans et al. 2008, Chase 2010, Hurlbert and Jetz 2010). The research presented here therefore yields some of the most thorough macroecological investigations of spatial and temporal β -diversity to date by combining a β -diversity metric relatively insensitive to changes in local and regional diversity, while incorporating environmental information of natural communities across a latitudinal gradient in North America.

2.2 Methods

Beginning in late May and concluding in late July from 2012-2014, we sampled the zooplankton communities (cladocerans, copepods, and rotifers) from fishless

ponds at 10 different regions/latitudes across North America (Figure 2.1, Table 2.1). The one exception was our lowest latitude site, which was sampled in October during the rainy season, which ensured that the temporary fishless ponds were filled (most, if not all, permanent ponds in the area have fish). Our goal was to sample at least five ponds from each site per year, but some had to be skipped due to drought conditions in 2013 or 2014 (Table 2.2).

All 10 regions were located in relatively natural areas (1 national park, 2 university research stations, 1 state conservation area, 2 national grasslands, 2 state parks, and 2 provincial parks) and spanned from 28.50°N to 53.65°N (Table 2.1). The sites were chosen based on similar spatial/landscape characteristics to limit the potential biases they could cause in our analyses, and the ponds are separated by relatively short distances (all 5 ponds were within a 15 km area) to limit isolation effects on spatial β -diversity.

Zooplankton sampling consisted filtering 10 L of pond water through an 80 μ m plankton net, with each liter coming from a different spot in the pond. Because zooplankton communities can vary substantially with depth and habitat (Kalff 2002), we limited the area of the pond sampled to that which was one meter or less deep and mainly in the littoral zone with submerged and emergent vegetation. The 10 L of filtered water were captured in a 50-mL centrifuge tube and preserved with acid Lugols for later identification in the laboratory. Identification was made to the lowest taxonomic classification (mostly to species) using a compound microscope.

In addition to sampling the zooplankton communities we assessed some aspects of the abiotic environment – percent canopy cover, pond size, emergent

vegetation cover, and estimated pond depth. We also collected 6, 50-mL water samples from each pond. These were used for analysis of total nitrogen and phosphorus, which tend to be good predictors of plant biomass and productivity, as well as zooplankton biomass (e.g. Schindler 1978, Smith 1979, Hanson and Peters 1984, Pace 1986). Because organismal activity can quickly alter nutrient concentrations in small volumes, these were placed on ice while in the field, and then frozen in a portable freezer. Nutrient analysis was performed in the laboratory, using 35 - 100 mL of water per analysis. All water was first filtered through 35 μ m filter to remove sediments and plankton. Total nitrogen (TN) and phosphorus (TP) were analyzed using spectrophotometry after persulfate digestion (Wetzel and Likens 1991).

Because the number of ponds sampled varied from year to year for some regions, assessing any trends in regional richness with latitude required rarefaction based on the lowest number of sampling units across all regions (Drury-Mincy Conservation Area). Rarefaction for every other region proceeded by randomly selecting 9 samples (each pond in a given year is equal to one sample) and tallying the total number of species encountered across those sample. This was performed 500 times and averaged to result in an average rarefied richness for each region. The average richness was then related to latitude using a Pearson product-moment correlation test.

Because most ponds were sampled every year at each region, we could also quantify both temporal and spatial β -diversity. Here we used an additive metric based on a modified version of Hurlbert's (1971) probability of interspecific encounter (PIE).

PIE is similar to local diversity or evenness metrics and is in fact the complement of Simpson's diversity index D ; $PIE = 1 - D$. It specifically measures the probability of encountering a different species given a random sampling of an individual from the same species abundance distribution (SAD), and thus increasing PIE values indicate increasing diversity/evenness. PIE is also representative of the *initial* slope of the rarefaction curve (Lande 1996, Lande et al. 2000, Olszewski 2004, see Figure 2.2), meaning that it is relatively insensitive to the number of individuals in a sample. In addition, as it reflects the initial rate of increase only, PIE is much more sensitive to abundant species as compared to rare species, such that missed rare species do not result in misleading PIE values.

As with other entropy metrics, PIE values cannot be meaningfully compared among sites (Jost 2006), however, but must first be converted to an effective number of species (ENS). If all species had the same number of individuals, ENS would be the same as species richness; when communities are not completely even, ENS decreases. The conversion of PIE to an ENS is done with the following equation: $ENS_{pie} = 1 / \sum_{i=1}^S p_i^2$, where S is the number of species in a community, and p_i is the relative abundance of species i (Jost 2006, Dauby and Hardy 2012). Since it is an evenness metric, ENS_{pie} can be calculated at the local and regional level; the difference between which results in our β -diversity metric: $\beta\text{-pie} = \gamma\text{-pie} - \alpha\text{-pie}$ (see Figure 2.2B). In other words, $\beta\text{-pie}$ reflects the effective number of species gained (or lost, though this is uncommon) when going from a local to regional scale. It also quantifies how much local SAD's differ from regional species pools.

This metric was selected because it is relatively insensitive to variation in the size or shape of the regional SAD or to the sampling effort (number of individuals) of local communities (Olszewski 2004), which the most commonly used β -diversity metrics, such as the Bray-Curtis and Jaccard's indices, are not (Tuomisto 2010a, Tuomisto 2010b). The null model approached often employed when using such sensitive metrics is therefore not required with β -pie, as it already represents variation in community composition that would be expected if communities were assembled at random from the species pool. In fact β -pie may be an improvement over many null models, as recent research is revealing that many null models are not actually insensitive to the various sampling effects they attempt to account for (Mori et al. 2015, Tucker et al. 2015).

Spatial β -pie was calculated for each region/latitude in all three years with the exception of Drury-Mincy in 2013 and LBJ National Grasslands in 2014 (see Table 2.2). To maintain consistent sample size within a year, any ponds that were not sampled in 2013 that were sampled in 2012 (i.e. at Turtle Mountain, Itasca, and Fort Pierre) were excluded from the 2012 analysis. Because only 4 ponds were sampled in 2014 at several sites due to drying or access issues, one pond was selected at random and excluded from any regions that had five ponds sampled that year (i.e. Elk Island, Rumsey, Lux Arbor, and Busch).

Temporal β -pie was calculated for each pond that was sampled all three years (N=37). For these calculations, α -pie was calculated the same as for space, but γ -pie consisted of all organisms found in the same pond across all three years. This yielded three temporal β -pie values for each pond corresponding to each year. Finally for

each pond that was sampled multiple years, (N=48) we investigated the correlation between the average spatial and temporal β -pie.

Spatial and temporal β -pie values represent the combined effect of deterministic species interactions, environmental variation, and dispersal limitation on community composition. Spatial and temporal β -pie values were thus regressed against latitude to indicate if there are any systematic changes in β -pie (independent of local community size or regional SAD) with latitude. No significant relationship between latitude and β -pie would indicate that processes creating significant aggregation do not vary systematically with latitude. In contrast, a positive relationship between latitude and β -pie would indicate increasing importance of those processes, while a negative relationship would indicate the opposite. For spatial β -pie, this analysis was an ordinary least squares regression. Because our temporal data appeared to violate the assumption of homoscedasticity, we performed a linear regression with robust parameter estimation on the relationship between latitude and temporal β -pie. Robust regression uses maximum likelihood estimators (MM-estimators) to assess if any data points are given too much weight to the analysis. Any identified points are then excluded from the regression.

We further performed a principal components regression (PCR) using our environmental data to assess which factors most deterministically influenced spatial and temporal turnover. All variables were log-transformed and scaled (mean = 0, standard deviation = 1) prior to the principal components analysis (PCA). For the principal components regression, we used the number of components indicated by the Kaiser criterion (1960), which retains only the factors with eigenvalues greater

than one. This analysis indicates which, if any, of the measured environmental variables is related to spatial or temporal β -pie. No PCR was performed for 2014 due to heavy loss of water samples and nutrient data because of a malfunctioning portable freezer.

Table 2.1. Sampling locations of ponds from 2012-2014.

Area	Latitude (°N)	Longitude (°W)
Elk Island National Park	53.65	112.87
Rumsey Natural Area	51.88	112.62
Turtle Mountain Provincial Park	49.30	100.25
Itasca State Park	47.54	95.26
Fort Pierre National Grasslands	44.44	100.25
Lux Arbor Reserve	42.63	85.22
Busch Conservation Area	38.71	90.74
Drury-Mincy Conservation Area	36.52	93.08
LBJ National Grasslands	33.35	97.59
University of Central Florida Natural Areas	28.50	81.38

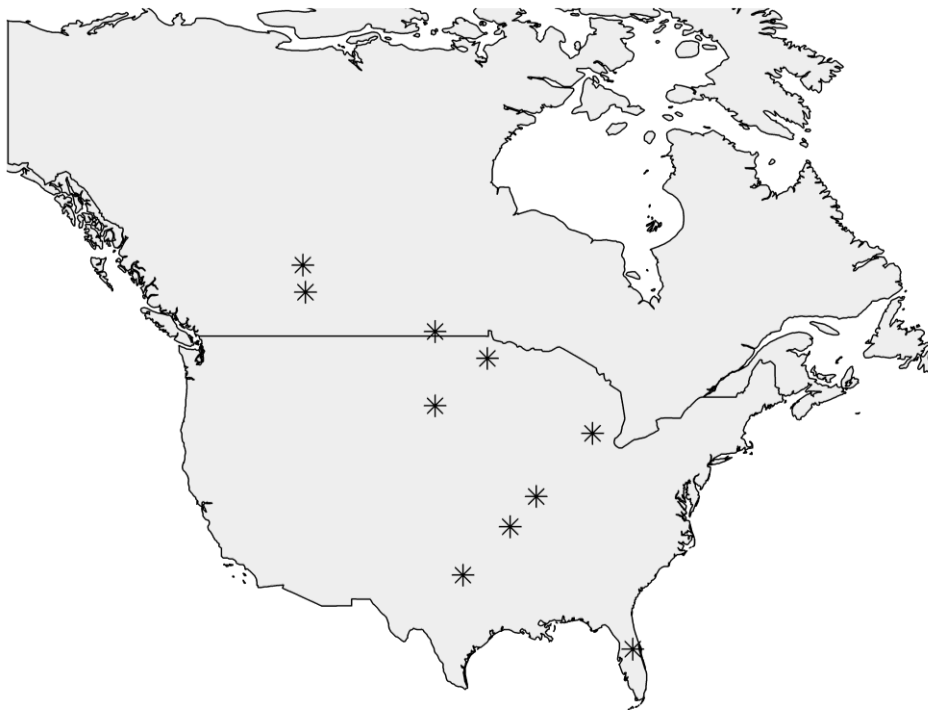


Figure 2.1. Locations of ponds sampled annually for zooplankton from 2012-2014.

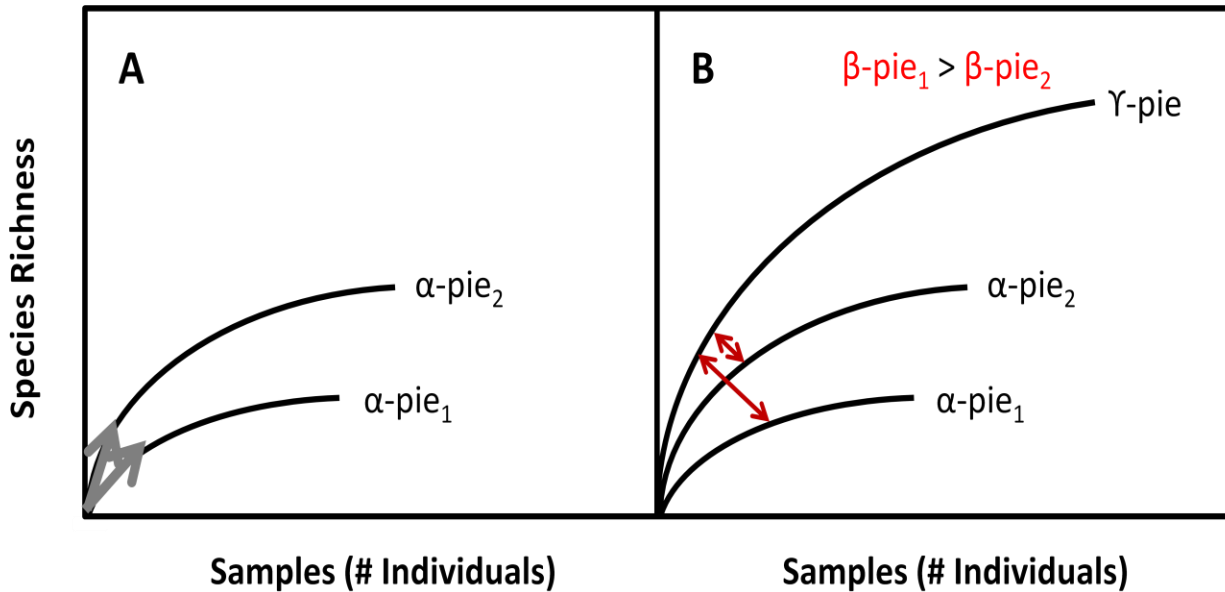


Figure 2.2. Species accumulation curves for a region consisting of two communities. A) The probability of interspecific encounter (PIE) for each local community is the initial slope of each curve, as represented by the gray arrows. B) PIE is found at the regional level in the same manner by combining all individuals across both communities into a single pool. The difference between the initial slope of each local (α) curve and the regional (γ) curve is $\beta\text{-pie}$, or aggregation, and is represented by the red arrows.

2.3 Results

First, we examined any relationship between species richness and latitude, which, due to some ponds drying in 2013 and 2014, required sample-based rarefaction. This yielded a significant negative correlation between rarefied regional richness and latitude ($r = -0.68$, $N = 10$, $p = 0.03$; Figure 2.3).

The relationship between spatial β -pie and latitude varied across years (Table 2.3, Figure 2.4). In 2012, there was a significant negative relationship between spatial β -pie and latitude ($p < 0.001$), but this reversed in 2013 ($p < 0.0001$). In 2014, there was no significant relationship ($p > 0.05$). Temporal β -pie was not significantly related to latitude in any of the sampled years ($p > 0.05$, Table 2.4, Figure 2.5). Finally, there was no significant correlation between the average spatial and temporal β -pie across all years for each pond ($r = -0.001$, $N = 48$, $p = 0.99$; Figure 2.6).

Six environmental variables were measured for each pond during each sampling: area (m^2), percent canopy cover, percent emergent vegetation cover (on the pond surface), estimated pond depth (m), total nitrogen (TN, $\mu g L^{-1}$), and total phosphorus (TP, $\mu g L^{-1}$). Due to multicollinearity among variables, we performed a principal component analysis of the ponds for which we had all environmental data and for which we had an appropriate spatial or temporal β -pie value for that year. We did not have TN or TP measurements for some ponds in one or both years, which resulted in different sample sizes for the PCR's ($N = 42, 43$ for spatial β -pie in 2012 and 2013, respectively; $N = 30, 36$ for temporal β -pie in 2012 and 2013, respectively). We selected only those principal components that met the Kaiser criterion ($SD > 1.00$) in each PCR (Tables 2.5, 2.8, 2.11, 2.14). Of the PCR's only spatial β -pie was significantly related to the first principal component in 2012 (Table 2.7; $df = 3$ and 38 , $F = 4.272$, $adj\ r^2 = 0.193$, $p = 0.011$). The order of the absolute value of the loadings of the six tested variables in this analysis are the following from largest to smallest: area $>$ TN $>$ TP $>$ canopy cover $>$ depth $>$ vegetation cover (Table 2.6). Spatial β -pie was not significantly related to the tested components in 2013 (Table 2.13; $df = 3$ and 39 , $F = 0.486$, $adj\ r^2 = -0.038$, $p =$

0.694), and neither was temporal β -pie in either 2012 (Table 2.10; $df = 2$ and 27 , $F = 0.780$, $\text{adj } r^2 = -0.015$, $p = 0.469$) or 2013 (Table 2.16; $df = 3$ and 32 , $F = 0.519$, $\text{adj } r^2 = -0.043$, $p = 0.672$). The PCA loadings for the environmental variables in those years are presented in Tables 2.12, 2.9, and 2.15, respectively.

Table 2.2. Number of ponds sampled each year from 2012-2014.

Area	2012	2013	2014
Elk Island National Park	5	5	5
Rumsey Natural Area	5	5	5
Turtle Mountain Provincial Park	5	5	4
Itasca State Park	5	5	4
Fort Pierre National Grasslands	5	5	4
Lux Arbor Reserve	5	5	5
Busch Conservation Area	5	5	5
Drury-Mincy Conservation Area	5	0	4
LBJ National Grasslands	5	5	1
University of Central Florida Natural Areas	5	5	4

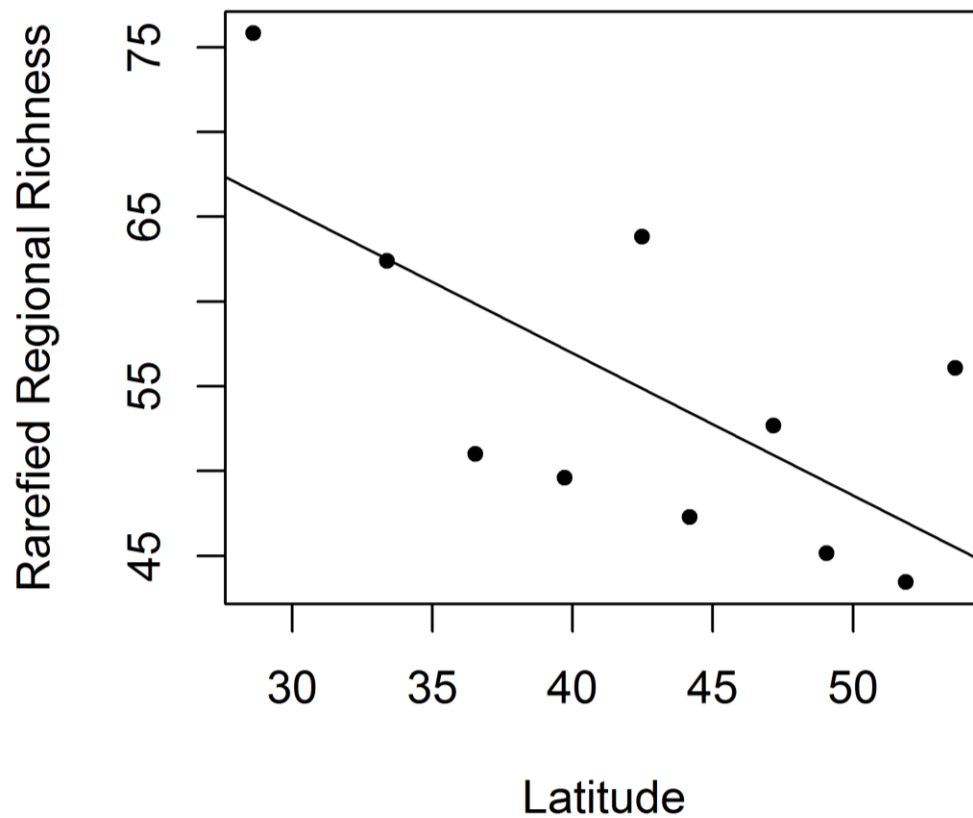


Figure 2.3. The relationship between average rarefied regional richness and latitude. The average richness of 500 simulations with 9 random subsamples per region is reported.

Table 2.3. Linear regression statistics for the relationship between latitude and spatial β -pie from 2012-2014.

Year	df	SE	F	t	Adjusted r^2	p
2012	48	0.0690	12.7	3.563	0.1927	0.0008
2013	43	0.0691	23.0	-4.797	0.3335	< 0.0001
2014	34	0.0939	1.34	-1.158	0.0096	0.2551

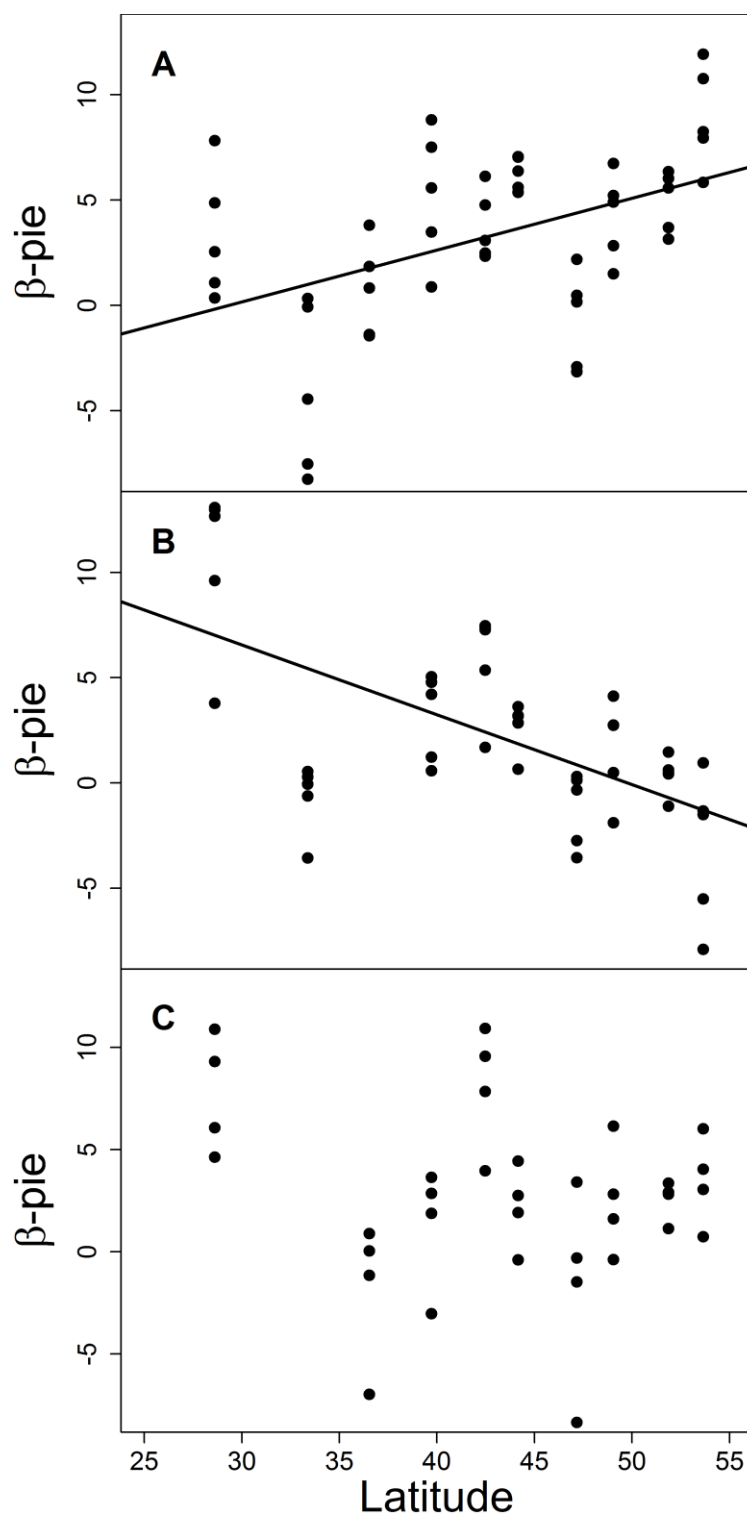


Figure 2.4. Spatial β -pie as a function of latitude for ponds sampled in A) 2012, B) 2013, and C) 2014. Linear regression lines included when the relationship was significant ($p < 0.05$).

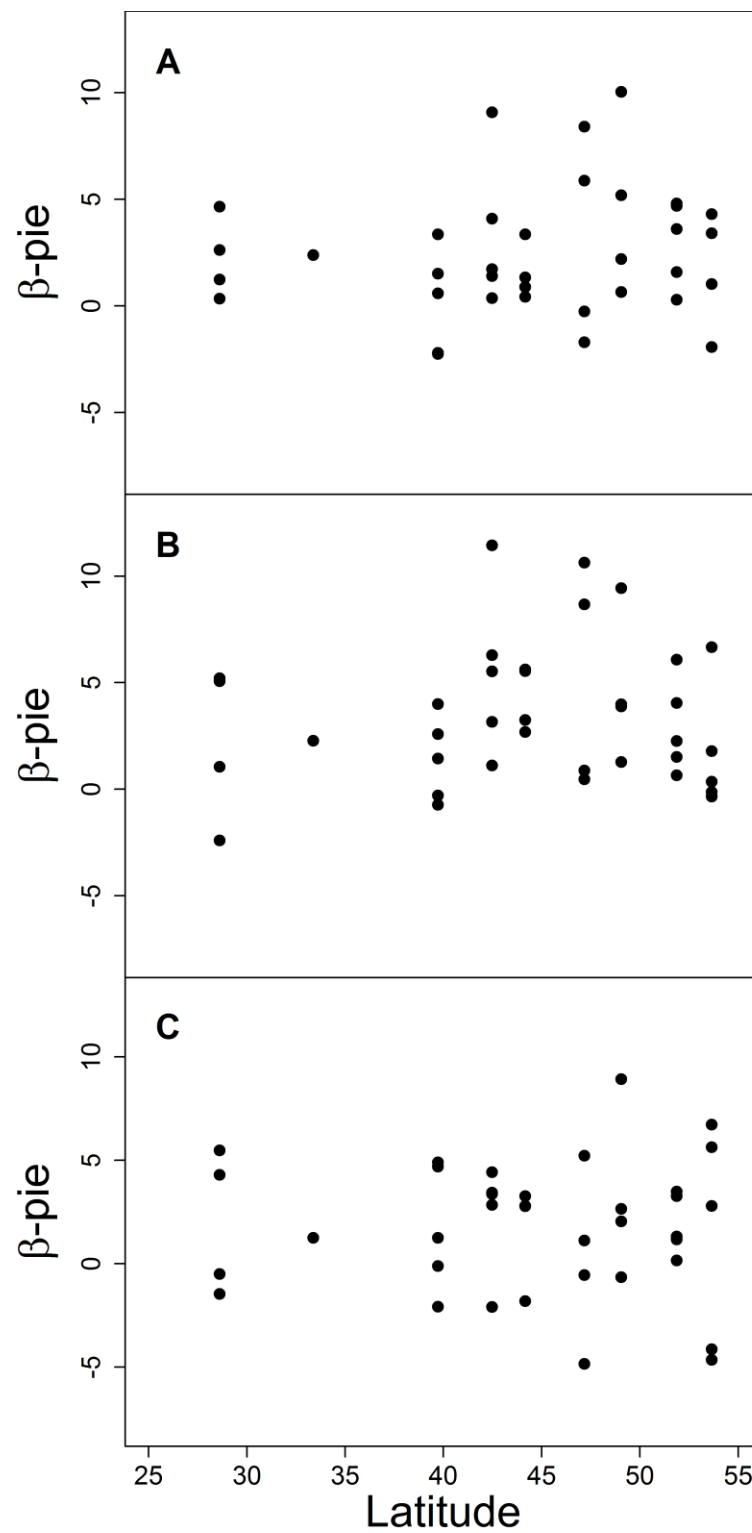


Figure 2.5. Temporal β -pie as a function of latitude for ponds sampled in A) 2012, B) 2013, and C) 2014.

Table 2.4. Robust linear regression statistics for the relationship between latitude and temporal β -pie from 2012-2014.

Year	df	SE	t	Adjusted r^2	p
2012	34	0.0468	0.712	-0.0196	0.481
2013	33	0.0724	0.169	-0.0276	0.867
2014	34	0.0793	-0.012	-0.0287	0.99

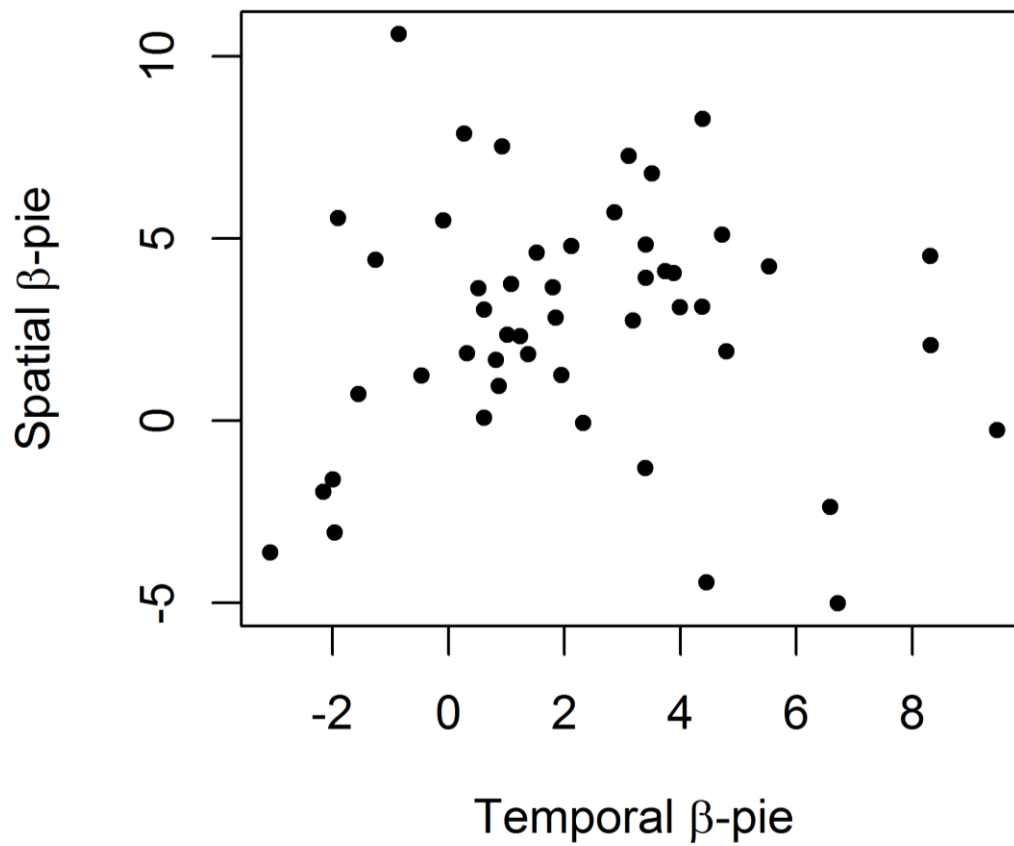


Figure 2.6. The relationship between the average temporal β -pie and spatial β -pie for each pond across all years.

Table 2.5. Importance of components for the Principal Component Analysis of 6 environmental variables of ponds (N = 42) analyzed for spatial β -pie in 2012.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard Deviation	1.449	1.158	1.007	0.875	0.659	0.588
Proportion of Variance	0.350	0.224	0.169	0.128	0.072	0.058
Cumulative Proportion	0.350	0.574	0.742	0.870	0.942	1.000

Table 2.6. PCA loadings for the 6 environmental variables measured for ponds (N = 42) analyzed for spatial β -pie in 2012. Only the first three component loadings are presented based on the Kaiser criterion (Table 2.5, SD > 1.00).

	Area	Canopy Cover	Vegetation Cover	Depth	NTL	PTL
PC1	0.523	-0.335	0.145	0.318	0.497	0.495
PC2	-0.253	0.375	0.318	-0.602	0.418	0.396
PC3	0.210	-0.220	0.861	-0.132	-0.221	-0.315

Table 2.7. Principal component regression statistics for the relationship between the values of the first three principal components of the ponds (N = 42) sampled in 2012 for spatial β -pie.

	Estimate	SE	t	p
PC1	1.285	0.420	3.057	< 0.01
PC2	-0.978	0.526	-1.860	< 0.10
PC3	-0.063	0.605	-0.104	0.917

Table 2.8. Importance of components for the principal component analysis of 6 environmental variables of ponds (N = 30) analyzed for temporal β -pie in 2012.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard Deviation	1.391	1.195	0.995	0.878	0.796	0.491
Proportion of Variance	0.322	0.238	0.165	0.129	0.106	0.040
Cumulative Proportion	0.322	0.561	0.726	0.854	0.960	1.000

Table 2.9. PCA loadings for the 6 environmental variables measured for ponds (N = 30) analyzed for temporal β -pie in 2012. Only the first two component loadings are presented based on the Kaiser criterion (Table 8, SD > 1.00).

	Area	Canopy Cover	Vegetation Cover	Depth	NTL	PTL
PC1	0.337	-0.051	0.351	-0.192	0.570	0.632
PC2	-0.323	0.594	0.437	-0.574	-0.112	-0.095

Table 2.10. Principal component regression statistics for the relationship between the values of the first two principal components of the ponds (N = 30) sampled in 2012 for temporal β -pie.

	Estimate	SE	t	p
PC1	0.238	0.376	0.633	0.532
PC2	0.471	0.437	1.077	0.291

Table 2.11. Importance of components for the principal component analysis of 6 environmental variables of ponds (N = 43) analyzed for spatial β -pie in 2013.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard Deviation	1.258	1.120	1.044	0.885	0.789	0.700
Proportion of Variance	0.264	0.239	0.182	0.131	0.104	0.0816
Cumulative Proportion	0.264	0.503	0.684	0.815	0.918	1.000

Table 2.12. PCA loadings for the 6 environmental variables measured for ponds (N = 43) analyzed for spatial β -pie in 2013. Only the first three component loadings are presented based on the Kaiser criterion (Table 2.11, SD > 1.00).

	Area	Canopy Cover	Vegetation Cover	Depth	NTL	PTL
PC1	0.497	0.158	0.631	0.163	0.537	-0.122
PC2	-0.456	0.518	0.123	-0.599	0.347	0.172
PC3	0.255	-0.444	0.065	-0.2856	0.086	0.803

Table 2.13. Principal component regression statistics for the relationship between the values of the first three principal components of the ponds (N = 43) sampled in 2013 for spatial β -pie.

	Estimate	SE	t	p
PC1	0.0361	0.570	0.063	0.950
PC2	0.123	0.599	0.206	0.838
PC3	-0.816	0.687	-1.188	0.242

Table 2.14. Importance of components for the principal component analysis of 6 environmental variables of ponds (N = 36) analyzed for temporal β -pie in 2013.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard Deviation	1.254	1.170	1.054	0.877	0.847	0.680
Proportion of Variance	0.262	0.228	0.185	0.128	0.120	0.077
Cumulative Proportion	0.262	0.490	0.675	0.804	0.923	1.000

Table 2.15. PCA loadings for the 6 environmental variables measured for ponds (N =36) analyzed for temporal β -pie in 2013. Only the first three component loadings are presented based on the Kaiser criterion (Table 2.15, SD > 1.00).

	Area	Canopy Cover	Vegetation Cover	Depth	TN	TP
PC1	0.676	-0.224	0.475	0.474	0.180	-0.099
PC2	-0.007	0.572	0.416	-0.370	0.601	-0.026
PC3	0.204	-0.311	0.064	-0.351	0.073	0.854

Table 2.16. Principal component regression statistics for the relationship between the values of the first three principal components of the ponds (N = 36) sampled in 2013 for temporal β -pie.

	Estimate	SE	t	p
PC1	0.015	0.448	0.033	0.974
PC2	0.548	0.481	1.140	0.263
PC3	0.270	0.534	0.506	0.616

2.4 Discussion

For both spatial and temporal β -pie, there were many instances of aggregation (non-zero β -pie values), and β -pie values tend to be more positive than negative (Figures 2.4-2.5). The relatively few communities with negative β -pie values indicate overdispersion at the local level relative to the regional pool, wherein local communities have more evenly distributed SAD's than the overall regional SAD. Because negative values are much less common, however, these results show that species are often clumped, rather than overdispersed, in space and time.

In contrast to other studies, we found no consistent trends of spatial or temporal β -diversity with latitude. This could be the result of the metric used, the taxonomic group investigated, or the scale of the investigations. Although we did find a significant negative relationship between species richness and latitude (Figure 2.3), zooplankton are a group of species that have been suggested to have a reverse latitudinal diversity gradient, where species richness may *increase* with latitude (Hillebrand and Azovsky 2001). We hypothesize, however, that our opposing result comes from our selection of habitat sampled, which stayed relatively similar across latitudes. That is, we only sampled fishless ponds of a certain size (<100m in diameter) and from only a limited pond depth (<1m). This possibly eliminated a large suite of species that inhabit large freshwater lakes of varying depths that increase in area and frequency with latitude in North America (Kalff 2002). This limitation to relatively small ponds was not done in the other known zooplankton study that found a negative relationship between temporal β -diversity and latitude (Shurin et al. 2007), although the authors did find that temporal β -

diversity was not affected by lake area. Korhonen et al. (2010) also studied aquatic communities (though not specifically zooplankton) and assessed temporal turnover as a function of, among other variables, ecosystem size and latitude. However, they did not separate different types of aquatic communities (i.e. marine, lake, or stream) or different sizes of aquatic organisms in their analysis finding a significant negative relationship between interannual temporal turnover and latitude. In addition, neither of these studies attempted to account for the numerical dependence of α -, β -, and γ -diversity (Baselga 2007).

With respect to spatial β -diversity, in the first year of sampling, spatial β -pie significantly increased with latitude, the following year it significantly decreased with latitude, and finally the third year there was no significant relationship. Unlike Soininen et al. (2007) but similar to Kraft et al. (2011), these results suggest there may not be consistent trends between latitude and the assembly mechanisms that affect community compositional turnover in space (as measured by our β -diversity metric). Instead, perhaps interannual variation in environmental or biotic factors play a major role in any trends between β -diversity and latitude. Although long-term datasets are becoming increasingly available, especially for tree communities, it may take decades or centuries of sampling communities with such long generation times to repeat these results. Nevertheless, we recognize that three years of data with 4-5 communities per region may not be sufficient to detect any relatively weak signals of spatial and temporal β -pie with latitude.

Also dissimilar to other studies, we did not see a significant relationship between spatial and temporal turnover (Ptacnik et al. 2008, Ptacnik et al. 2010, Stegen et al.

2013). However, this might be expected as Stegen et al. (2013) found that their strong positive relationship was dampened after they implemented a null model to account for numerical sampling effects from the regional pool. Indeed, in a theoretical model, Steiner & Leibold (2004) showed that stochastic dispersal in a metacommunity resulted in a positive relationship between spatial and temporal turnover. Since β -pie essentially eliminates stochastic sampling effects, this could explain the lack of a significant trend between spatial and temporal turnover.

Finally, during the first 2 years of sampling, aggregation does not appear to be driven consistently by the measured environmental variables. The one exception was in 2012, wherein the first principal component, which was mostly related to the area of the pond and the total amount of nitrogen and phosphorus in the pond's water column, significantly affected spatial β -pie. All three of these variables had positive PC1 loadings, indicating the ponds with larger area, or high TN and TP also tended to have high turnover in space relative to the regional SAD in 2012. One cautious interpretation is that larger and presumably more productive ponds select for different types of species compared to other ponds in the region. In fact, some studies have shown that spatial turnover increases with primary production (e.g. Chase et al. 2000, Chase and Leibold 2002, but see Bonn et al. 2004, Gaston et al. 2007, Hurlbert and Jetz 2010). However, because these results are inconsistent across years and because nutrient levels are a proxy for productivity, we caution any strong inference of their effect on spatial turnover.

Despite no clear trends in spatial or temporal β -pie with latitude, with each other, or with specific environmental variables, this research gives a valuable macroecological

perspective on community assembly. Importantly, finding no consistent trends cautions any mechanistic interpretation of significant relationships found between regional or local diversity (often correlated with latitude) and a given β -diversity metric. Further, most observational β -diversity research is on spatial patterns at single snapshots in time (Micheli et al. 1999, Bolliger et al. 2007), but this study highlights that trends can change relatively rapidly over time. Indeed there are likely many mechanisms affecting community assembly in natural systems which interact and shift in importance both in space and time in heretofore unrealized ways. We suggest that gathering more long-term data and performing macroecological experiments aimed to detect specific assembly mechanisms may aid in closing the gaps in large-scale community assembly dynamics.

2.5 References

- Adler, P. B. and W. K. Lauenroth. 2003. The power of time: spatiotemporal scaling of species diversity. *Ecology Letters* **6**:749-756.
- Adler, P. B., E. P. White, W. K. Lauenroth, D. M. Kaufman, A. Rassweiler, and J. A. Rusak. 2005. Evidence for a general species-time-area relationship. *Ecology* **86**:2032-2039.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters* **14**:19-28.
- Baselga, A. 2007. Disentangling distance decay of similarity from richness gradients: response to Soininen et al. 2007. *Ecography* **30**:838-841.
- Beisner, B. E., P. R. Peres, E. S. Lindstrom, A. Barnett, and M. L. Longhi. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* **87**:2985-2991.
- Bolliger, J., H. H. Wagner, and M. G. Turner. 2007. Identifying and quantifying landscape patterns in space and time. Pages 177-194 *in* F. Kienast, O. Wildi, and S. Ghosh, editors. *A changing world: Challenges for landscape research*. Springer, New York.

- Bonn, A., D. Storch, and K. J. Gaston. 2004. Structure of the species-energy relationship. *Proceedings of the Royal Society B-Biological Sciences* **271**:1685-1691.
- Chalcraft, D. R., J. W. Williams, M. D. Smith, and M. R. Willig. 2004. Scale dependence in the species-richness-productivity relationship: The role of species turnover. *Ecology* **85**:2701-2708.
- Chase, J. M. 2003. Community assembly: when should history matter? *Oecologia* **136**:489-498.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* **104**:17430-17434.
- Chase, J. M. 2010. Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science* **328**:1388-1391.
- Chase, J. M. and T. M. Knight. 2013. Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters* **16**:17-26.
- Chase, J. M. and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* **416**:427-430.
- Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* **81**:2485-2497.

- Chase, J. M. and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **366**:2351-2363.
- Condit, R., N. Pitman, E. G. Leigh, J. Chave, J. Terborgh, R. B. Foster, P. Nunez, S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos, and S. P. Hubbell. 2002. Beta-diversity in tropical forest trees. *Science* **295**:666-669.
- Dahl, C., V. Novotny, J. Moravec, and S. J. Richards. 2009. Beta diversity of frogs in the forests of New Guinea, Amazonia and Europe: contrasting tropical and temperate communities. *Journal of Biogeography* **36**:896-904.
- Dauby, G. and O. J. Hardy. 2012. Sampled-based estimation of diversity sensu stricto by transforming Hurlbert diversities into effective number of species. *Ecography* **35**:661-672.
- Davidar, P., B. Rajagopal, D. Mohandass, J. P. Puyravaud, R. Condit, S. J. Wright, and E. G. Leigh. 2007. The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography* **16**:510-518.
- De Caceres, M., P. Legendre, R. Valencia, M. Cao, L. W. Chang, G. Chuyong, R. Condit, Z. Q. Hao, C. F. Hsieh, S. Hubbell, D. Kenfack, K. P. Ma, X. C. Mi, M. N. S. Noor, A. R. Kassim, H. B. Ren, S. H. Su, I. F. Sun, D. Thomas, W. H. Ye, and F. L. He. 2012. The variation of tree beta diversity across a global network of forest plots. *Global Ecology and Biogeography* **21**:1191-1202.

- Evans, K. L., S. E. Newson, D. Storch, J. J. D. Greenwood, and K. J. Gaston. 2008. Spatial scale, abundance and the species-energy relationship in British birds. *Journal of Animal Ecology* **77**:395-405.
- Fukami, T. 2015. Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. *Annual Review of Ecology, Evolution, and Systematics* **46**:1-23.
- Gaston, K. J., R. G. Davies, C. D. L. Orme, V. A. Olson, G. H. Thomas, T. S. Ding, P. C. Rasmussen, J. J. Lennon, P. M. Bennett, I. P. F. Owens, and T. M. Blackburn. 2007. Spatial turnover in the global avifauna. *Proceedings of the Royal Society B-Biological Sciences* **274**:1567-1574.
- Gilbert, B. and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences of the United States of America* **101**:7651-7656.
- Hanson, J. M. and R. H. Peters. 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:439-445.
- Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* **61**:151-158.
- Hillebrand, H. and A. I. Azovsky. 2001. Body size determines the strength of the latitudinal diversity gradient. *Ecography* **24**:251-256.
- Hubbell, S. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton, NJ.

- Hurlbert, S.H., 1971, The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, v. 52, p. 577-586. (On explicit calculation of rarefaction richness and derivation of Hurlbert's PIE measure of evenness.)
- Hurlbert, A. H. and W. Jetz. 2010. More than "More Individuals": The Nonequivalence of Area and Energy in the Scaling of Species Richness. *American Naturalist* **176**:E50-E65.
- Jost, L. 2006. Entropy and diversity. *Oikos* **113**:363-375.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* **88**:2427-2439.
- Jurasinski, G., V. Retzer, and C. Beierkuhnlein. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia* **159**:15-26.
- Kalff, J. 2002. *Limnology: Inland Water Ecosystems*. Prentice Hall, Upper Saddle River, NJ.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003a. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* **72**:367-382.
- Koleff, P., J. J. Lennon, and K. J. Gaston. 2003b. Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* **12**:483-498.
- Korhonen, J. J., J. Soininen, and H. Hillebrand. 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology* **91**:508-517.
- Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A.

- L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science* **333**:1755-1758.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76**:5-13.
- Lande, R., P. J. DeVries, and T. R. Walla. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos* **89**:601-605.
- Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjornstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. *Oikos* **85**:161-169.
- Mori, A. S., S. Fujii, R. Kitagawa, and D. Koide. 2015. Null model approaches to evaluating the relative role of different assembly processes in shaping ecological communities. *Oecologia* **178**:261-273.
- Myers, J. A., J. M. Chase, I. Jimenez, P. M. Jorgensen, A. Araujo-Murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters* **16**:151-157.
- Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* **104**:377-387.
- Pace, M. L. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnology and Oceanography* **31**:45-55.

- Ptácník, R., T. Andersen, P. Brettum, L. Lepistö, and E. Willén. 2010. Regional species pools control community saturation in lake phytoplankton. *Proc Biol Sci.*
- Ptácník, R., A. G. Solimini, T. Andersen, T. Tamminen, P. Brettum, L. Lepistö, E. Willén, and S. Rekolainen. 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. *Proceedings of the National Academy of Sciences of the United States of America* **105**:5134-5138.
- Qian, H., J. D. Fridley, and M. W. Palmer. 2007. The latitudinal gradient of species-area relationships for vascular plants of North America. *American Naturalist* **170**:690-701.
- Qian, H. and R. E. Ricklefs. 2007. A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters* **10**:737-744.
- Qian, H. and X. L. Wang. 2015. Global relationships between beta diversity and latitude after accounting for regional diversity. *Ecological Informatics* **25**:10-13.
- Raup, D. M. and R. E. Crick. 1979. Measurement of Faunal Similarity in Paleontology. *Journal of Paleontology* **53**:1213-1227.
- Ricotta, C. 2010. On beta diversity decomposition: Trouble shared is not trouble halved. *Ecology* **91**:1981-1983.
- Schindler, D. W. 1978. Factors Regulating Phytoplankton Production and Standing Crop in World's Freshwaters. *Limnology and Oceanography* **23**:478-486.
- Shurin, J. B., S. E. Arnott, H. Hillebrand, A. Longmuir, B. Pinel-Alloul, M. Winder, and N. D. Yan. 2007. Diversity-stability relationship varies with latitude in zooplankton. *Ecology Letters* **10**:127-134.

- Smith, V. H. 1979. Nutrient Dependence of Primary Productivity in Lakes. *Limnology and Oceanography* **24**:1051-1064.
- Soininen, J., J. J. Lennon, and H. Hillebrand. 2007. A multivariate analysis of beta diversity across organisms and environments. *Ecology* **88**:2830-2838.
- Stegen, J. C., A. L. Freestone, T. O. Crist, M. J. Anderson, J. M. Chase, L. S. Comita, H. V. Cornell, K. F. Davies, S. P. Harrison, A. H. Hurlbert, B. D. Inouye, N. J. B. Kraft, J. A. Myers, N. J. Sanders, N. G. Swenson, and M. Vellend. 2013. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. *Global Ecology and Biogeography* **22**:202-212.
- Steiner, C. F. and M. A. Leibold. 2004. Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. *Ecology* **85**:107-113.
- Tucker, C. M., L. G. Shoemaker, K. F. Davies, D. R. Nemergut, and B. A. Melbourne. 2016. Differentiating between niche and neutral assembly in metacommunities using null models of beta-diversity. *Oikos* **125**:778-789.
- Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* **33**:2-22.
- Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* **299**:241-244.
- Vellend, M., D. S. Srivastava, K. M. Anderson, C. D. Brown, J. E. Jankowski, E. J. Kleynhans, N. J. B. Kraft, A. D. Letaw, A. A. M. Macdonald, J. E. Maclean, I. H. Myers-Smith, A. R. Norris, and X. X. Xue. 2014. Assessing the relative

- importance of neutral stochasticity in ecological communities. *Oikos* **123**:1420-1430.
- Vellend, M., K. Verheyen, K. M. Flinn, H. Jacquemyn, A. Kolb, H. Van Calster, G. Peterken, B. J. Graae, J. Bellemare, O. Honnay, J. Brunet, M. Wulf, F. Gerhardt, and M. Hermy. 2007. Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *Journal of Ecology* **95**:565-573.
- Wetzel, R. and G. Likens. 1991. *Limnological Analyses*. 2nd edition. Springer-Verlag, New York.
- Whittaker, R. 1967. Gradient Analysis of Vegetation. *Biological Reviews* **42**:207-264.
- Xu, W. B., G. K. Chen, C. R. Liu, and K. P. Ma. 2015. Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Global Ecology and Biogeography* **24**:1170-1180.

Chapter 3: The effect of drought on intraspecific aggregation varies with latitude but depends on dispersal ability

3.1 Introduction

The role of ecological processes in differentially influencing species and communities across latitudes has a long history in ecology and evolutionary biology. One of the most prominent ideas about ecological influence across latitudes is the tendency for environmental harshness and variability to increase with latitude, such that high latitude communities tend to be more environmentally limited relative to the more benign and stable conditions of low latitude environments. These ideas are evident as far back as Wallace (1878) who noted that intermittent glaciation periods may create a latitudinal gradient in the influence of the abiotic environment. Similarly, Dobzhansky (1950) and Fischer (1960) emphasized the increasing role of environmental harshness and variability with latitude, resulting in fewer, more generalist high latitude species that can cope with short-term seasonality and long-term climatic variability typical of high latitude environments. Despite this long history in recognizing the role of environmental filtering (i.e. the deterministic effects of the abiotic environment) on species traits during community assembly (Keddy 1992, Lavorel and Garnier 2002), and on community-wide diversity across latitudes (Pianka 1966, Mittelbach et al. 2007), there is relatively little known about the potential differential consequences environmental filtering may have

on the assembly of current ecological communities across latitudes (but see Qian and Ricklefs 2012, Myers et al. 2013, Qiao et al. 2015).

More recently, the potential role of stochasticity resulting in ecological drift in differentially affecting community composition has also been emphasized. In an ecological context, stochasticity can affect community composition and diversity patterns by causing changes in species abundances that are random with respect to species identity. Although the importance of stochastic processes and neutral models in ecology theory has long been recognized (MacArthur and Wilson 1963, Bell 2001, Chave 2004), Hubbell's neutral theory of biodiversity (2001) incited a surfeit of research on its potential influence in the last couple decades (Chave 2004, Alonso et al. 2006, Adler et al. 2007, McGill 2010, Rosindell et al. 2011, Matthews and Whittaker 2014). Neutral theory was controversial (and some might say successful) due to its ability to generate diversity patterns strikingly similar to those found extensively in nature using only three mechanisms-speciation, dispersal, and drift. Hubbell's work was primarily done in tropical tree communities, leading some ecologists to ask if the role of community assembly mechanisms, including stochasticity, might also vary with latitude (e.g. Qian et al. 2009, Schemske et al. 2009, Myers et al. 2013). Nevertheless, quantifying if and how stochasticity differentially affects communities across latitudes or regions that vary in local community or regional pool size, especially if there are also latitudinal gradients in non-stochastic ecological processes, such as environmental filtering, remains a major challenge in ecology (Chase and Myers 2011, Qian and Song 2013, Vellend et al. 2014, Mori et al. 2015, Xu et al. 2015, Tucker et al. 2016).

One approach that researchers have used to investigate the influence of stochasticity versus deterministic processes, such as environmental filtering, is by quantifying site to site variation in community composition, generally termed β -diversity. β -diversity is useful because it can be related to factors, such as spatial and environmental gradients, that are known to influence the assembly of ecological communities (Whittaker 1956, Bray and Curtis 1957, Gentry 1988, Tuomisto et al. 1995). For example, by measuring the same environmental variables in different regions for communities at the same spatial extent, researchers can quantify how much variance in community composition that spatial and environmental factors can explain (Legendre et al. 2005). However, due to incomplete information, much of the unexplained variance is likely a combination of unmeasured important environmental factors, historical effects, or simply stochasticity. For instance, even when the exact same environmental variables are being measured at the exact same spatial scale among regions, the magnitude of environmental gradients will most likely vary among regions. The result of this is that as gradients increase, there is greater opportunity for the environment to explain more variance. As no two regions likely to have the same environmental gradients, important environmental variables, spatial characteristics, or histories, such comparisons could be misleading.

In addition, quantifying β -diversity in a way that can/should be compared across regions is actively under debate. The main reason for this debate is that many β -diversity metrics are dependent on different aspects of regional (γ -) and/or local (α -) diversity (Jost 2006, 2007, Tuomisto 2010a). Because of these dependencies, it is difficult to conclude if β -diversity varies across regions because of numerical changes in

α - or γ -diversity, or if something of ecological interest during the community assembly process (e.g. dispersal limitation or the effect of environmental filtering), is driving compositional changes to varying degrees among regions. We generally call these dependencies of β - on α - and/or γ -diversity sampling effects, and for our purposes they reflect variation in β -diversity due to sampling a finite number of samples from a given distribution. The main approach that researchers take to correct for this is through null modeling, in which researchers simulate communities based on some null hypothesis about community assembly, calculate β -diversity for those simulated communities, and then see how much the observed values deviate from those simulated. This is convenient because if null model assumes stochastic assembly of local communities from a regional pool, then these simulated communities yield β -values expected if community assembly was purely stochastic. Any deviation from those is then interpreted as the result of non-stochastic, or deterministic, processes. However, recent research has shown the interpretation of null modeling can vary significantly depending on the β -diversity metric used and the structure of the null model, with different assumptions and metrics capturing the intended stochastic versus deterministic mechanisms to varying degrees (Mori et al. 2015, Xu et al. 2015, Tucker et al. 2016).

Here we present the results of an outdoor mesocosm experiment replicated at three latitudes/regions in North America-Florida (28.5°N), Missouri (38.5°N), and Alberta, Canada (51.0°N). The goal of the experiment was to assess 1) if the relative importance of stochasticity varied with latitude, and 2) if the effect of an environmental filter on community assembly varied with latitude. We used an approach similar to Chase (2007, 2010), in which mesocosms represented aquatic

pond communities that were assembled in a standardized manner across all three sites, which aimed to control for historical and spatial differences of communities among regions. After two years, we imposed a harsh environmental filter, drought, on half of the mesocosms per site, while leaving the remaining control mesocosms undisturbed. The year following the drought treatment, we assessed the degree to which the drought and control treatments deviated from a stochastic sampling expectation within each site using a less commonly used β -diversity metric, β -pie, which does not require null modeling for comparison across regions that differ in regional species abundance distributions (SAD's) or sampling effort among local communities. If drought affects all species equally, there should be no difference in aggregation between the drought and control treatments within a site. If drought restricts communities to a subset of drought-tolerant species, then the drought treatment will have lower aggregation than the controls. Alternatively, if drought disproportionately affects abundant species, allowing for rare species to increase, the drought treatment could actually increase aggregation.

These aggregation values were then compared across sites to assess whether the relative effect of the same environmental filter varied across the three latitudes. If the relative importance of stochasticity decreases with latitude, then the magnitude of β -pie values will increase with latitude. If high latitude communities are comprised of more generalist species that are more tolerant of environmental variability, then the relative effect of the drought treatment as compared to the controls on β -pie (as measured by an effect size) will decrease with latitude. If, however, high latitude

communities are less tolerant of drought, as might be expected due to a decrease in drought frequency with latitude, then the opposite pattern should occur.

Finally, we further compare these results for two different groups of species that vary in dispersal, active and passive dispersers. Because dispersal affects community assembly patterns and processes (Leibold et al. 2004, Weiher et al. 2011), the comparison of two dispersal groups will give further insight into the role of dispersal in mediating stochasticity and/or environmental filtering across latitudes.

3.2 Methods

3.2.1 Establishment

From March - June 2011, we established 20 outdoor mesocosms (2365-L cattle tanks) at each of three locations in North America - Orlando, FL; St Louis, MO; and Calgary, AB, Canada (Figure 3.1) - which were used to simulate aquatic pond communities. There were two assembly treatments, control and drought, which were initially assembled identically. All mesocosms received 5 cm of topsoil and was filled with well water. The topsoil and water originated from each experimental region and served to simulate the environmental conditions of that region. Topsoil provided nutrients within the range of observed nutrient levels (Nitrogen and Phosphorus measured for 10 ponds in each region) and ensured that aquatic plants, including macrophytes with root systems requiring soil, could establish in the mesocosms. After

filling with water, the mesocosms were inoculated with small numbers of aquatic organisms collected from 15 local ponds within the region. The initial inocula included macrophytes, pond sediments (including dormant stages of many aquatic organisms), mollusks, and crustaceans. For the macrophytes, 2-3 individuals of each species were planted in the soil. The other organisms were added after creating slurries of water or mud collected from the 15 local ponds. These homogenized slurries were then added to each mesocosms in the following quantities: 1L of mud, 50 mL of plankton (collected with a 80 μm net), and 250mL of invertebrates larger than 80 μm . The inoculations of few individuals aimed to simulate stochastic colonization events, giving rise to differences in mesocosm composition. The mesocosms were also left open to colonization from more mobile species, including insects in the orders Odonata (dragonfly and damselfly larvae), Coleoptera (beetles), Hemiptera (true bugs), allowing for the assembly of relatively complete aquatic pond communities.

3.2.2 Drought Treatment

From March – July in 2012, we imposed the drought treatment on 10 of the tanks in each region. Drought consisted of draining the tanks slowly over 4 weeks by using an L-shaped external PVC standpipe (2.54cm diameter x 0.6m tall), which could be incrementally lowered every few days. The gradual draining of the mesocosms were intended to simulate natural pond drying and give those organisms with the ability to respond to drying (e.g. exiting the pond or producing drought-tolerant resting stages) the opportunity to do so. The standpipe drain was covered with a 1mm plastic mesh to

prevent the loss of individuals through the drain. After fully emptied, the drought mesocosms remained dry for 1 month before being refilled with well water. Any rainfall that occurred during the dry month automatically drained out because the standpipe drain remained down (touching the ground) during that time. Because of variation in monthly precipitation averages among regions, the drought treatment occurred in April in Florida (before the rainy season) and in July-August in Missouri and Alberta, CA, after their peak rainfall.

3.2.3 Sampling

All mesocosms were sampled twice from March-July 2012 (pre-drought treatment) and 2013 (one year post-drought treatment) for macrophytes, zooplankton, and macroinvertebrates. Macrophyte composition was calculated as the average of two percent-cover estimates for each observed species per mesocosm. For the first year of sampling, this average was based on two different people's estimates, and the subsequent years it was the average of the same person's estimates on two different days. Percent cover estimates were done visually looking down at the surface of the mesocosms. Any species believed to have under 10% cover was estimated to the nearest 1%; any species above 10% was to the nearest 5% cover. This allowed for a mesocosm's total percent cover to be slightly above or significantly below 100% when there was a lot of unvegetated substrate. Zooplankton were sampled by filtering 5L of water collected from 5 different locations in the mesocosm through a 80 μ m plankton net. The plankton were preserved in an acid Lugols solution for later identification and

enumeration of species with a 10x compound microscope. Macroinvertebrates (> 80 μm) were sampled using two 0.36m diameter x1-m tall plastic cylinders, the bottom of which were plunged into benthic sediments to prevent the escape of any individuals from the cylinder during sampling. Dip-nets (0.33 mm mesh) were used to isolate individuals within a chimney until 5 consecutive empty net sweeps were achieved (Chase 2010). All macroinvertebrates per mesocosm were preserved in 70% ethanol for later identification and enumeration of species with a dissecting microscope. Any vertebrates (tadpoles) found during the macroinvertebrate sampling were identified and counted in the field and released back into the mesocosm. All macroinvertebrate individuals collected in the cylinders were identified to the lowest possible taxonomic level (either genus or species) and counted, yielding species abundance data.

3.2.4 Quantifying β -diversity

To determine if the drought treatment affected the degree of variation in community composition across regions/latitude, we used a modification of Hurlbert's (1971) probability of interspecific encounter (PIE). PIE gives the probability that any two individuals selected at random from the observed species abundance distribution (either locally or regionally) is of a different species. PIE is related to the more familiar Simpson's index D , wherein $\text{PIE} = 1 - D$, and thus a higher PIE indicates greater diversity/evenness in a sample. PIE is also numerically equivalent to the *initial* slope of a rarefaction curve, such that a higher PIE indicates a faster rate of increase in species richness with sampling effort (Olszewski 2004). As it reflects the initial rate of increase

only, PIE is very sensitive to abundant species and much less sensitive to rare species. This quality also makes it relatively insensitive to sampling effort at a community scale, i.e. the number of observed individuals in a local community (Lande et al. 2000, Olszewski 2004).

As a probability (ranging from 0 to 1), PIE is then used to quantify an effective number of species ($ENS_{pie} = 1 / \sum_{i=1}^S p_i^2$, where S is the number of species in a community, and p_i is the relative abundance of species i). The effective number of species is “the number of equally abundant species there would need to be in a sample to achieve the same diversity value as the one obtained,” and this conversion to ENS_{pie} allows for meaningful comparisons of values across communities or regions that vary in sampling (Jost 2006). Because we are interested in the relative role of regional versus local-scale processes on community composition, we quantified ENS_{pie} for each community (α -pie) and each treatment (γ -pie), as well as their difference (β -pie = γ -pie - α -pie). This latter number β -pie indicates the effective number of species gained (or lost, though this is uncommon) when going from a local to regional, or treatment, scale. Thus, β -pie values indicate the degree to which local community species abundance distributions deviate from regional pools. Furthermore, when individuals from the regional pool are distributed randomly to communities, β -pie values are at or near zero.

β -pie was selected for this study due to its numerical properties-namely that it is relatively insensitive to regional pool size or shape (SAD) and to the number of individuals observed in local communities (Olszewski 2004, Dauby and Hardy 2012, Chase and Knight 2013). These properties are particularly useful because the most commonly used β -diversity metrics, such as the Bray-Curtis and Jaccard's indices, are

sensitive to these factors (Tuomisto 2010a, Tuomisto 2010b). Unlike the null model approach, which compares observed and expected β -diversity values as an effect size that represents non-stochastic assembly, here any non-zero β -pie value already reflects variation in community composition that is not driven by sampling a finite and/or variable number of individuals from an observed species pool. Thus β -pie obviates the null model approach for the aspects of β -diversity in which we are most interested. It also appears to be an improvement over many null models, because recent research has found that null models do not always account for the sampling effects we are concerned with, namely community size (the number of individuals in a community) and regional SAD's (Mori et al. 2015, Tucker et al. 2015). For clarity and convenience, we henceforth call this aspect of β -diversity (β -pie) *aggregation*, though we do acknowledge that β -pie, can be negative, if a local community has a more even SAD compared to the regional pool. In this latter scenario a negative β -pie would indicate that the focal local community is *less* aggregated than expected given the regional species pool. Finally, because β -pie is simply the difference between γ -pie and α -pie, any non-zero value indicates that local community composition differs from that expected based solely on sampling from the regional species pool.

3.2.5 Analyses

For each unique region-treatment combination, ENSpie was quantified using all individuals identified per mesocosm (α -pie) and across all mesocosms per treatment (γ -pie). Aggregation (β -pie) was then quantified for each treatment-region combination as

the regional ENSpie minus the ENSpie of each mesocosm in that treatment.

Experiments replicated at different locations can have location be considered random or fixed, depending on if the locations are treated as a random blocking factors or if the investigator is interested in those specific locations (McIntosh 1983). Although the experiment was replicated at different locations, we were specifically interested in three individual regions at low, medium, and high latitudes in North America, which are not random samples of all levels of latitude. The experiment is not considered nested as nested experiments require subsamples of each replicate (Gotelli and Ellison 2004).

To test if aggregation varied among regions and assembly treatments, we therefore used a 2-factor ANOVA with both factors as fixed effects. We were specifically interested in the main effect of region, to see if aggregation varied across regions, and in the interaction term to see if the filtering treatment (relative to the control) differentially affected aggregation across regions. When a significant main effect of region or the interaction term was found, planned contrasts were then performed to examine which regions differed across both treatments, and, for the interaction term, which regions had significant differences in aggregation for the assembly treatment (drought and control). These analyses were performed separately for both dispersal groups to assess if dispersal mode qualitatively changed the models' results. To quantify the effect of the drought relative to controls, we also calculated an effect size measured as Cohen's d :

$$d = \frac{M_1 - M_2}{SD_{pooled}} ,$$

where M_1 and M_2 are the mean β -pie of the control and drought treatments, respectively, and the denominator is the pooled standard deviation across both treatments.

Because changes in β -pie can result from changes in α -pie γ -pie, or both, we also examined how γ -pie and α -pie changed across regions and treatments using the same 2-way ANOVA. Only one γ -pie value was available per treatment and region combination, so we first generated ten estimates of γ -pie to allow for statistical analysis with γ -pie estimates being the response variable. This was achieved by removing each of the replicate mesocosms and recalculating γ -pie for the remaining nine. The jackknifed γ -pie estimates and the observed α -pie values were the response variables for each model and for each dispersal group separately. All analyses were performed in R (version 3.1.2).

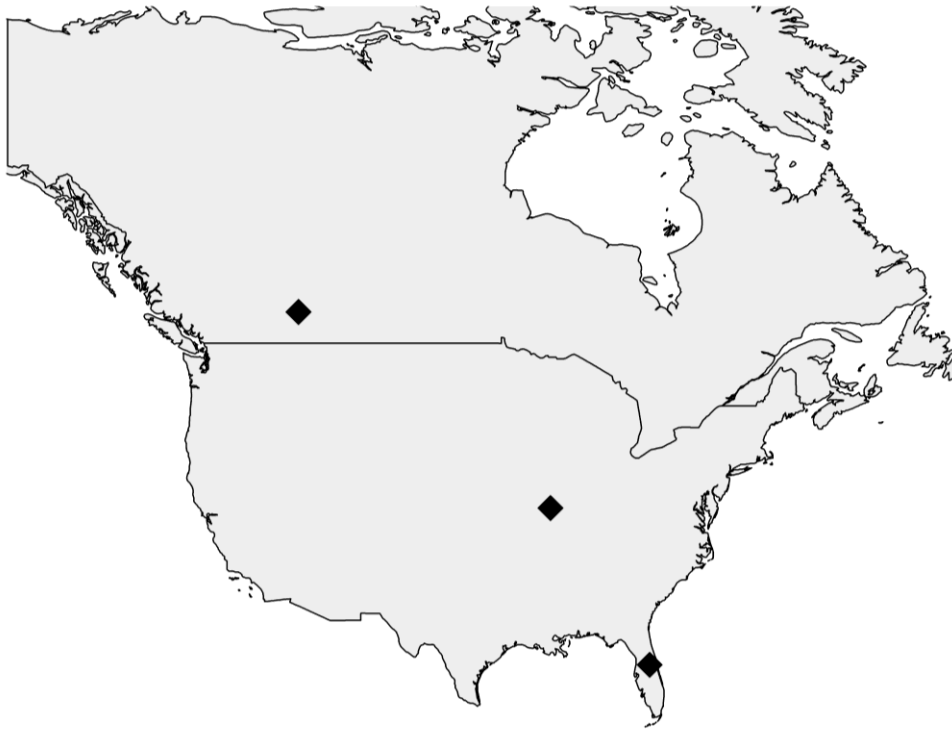


Figure 3.1. Map of experimental sites (◆). Sites correspond to latitudes of 28.5°N, 38.5°N, and 51.0°N.

3.3 Results

For both active and passive dispersers, there were significant main (Figures 3.2-3.3) and interactive effects of region and treatment on aggregation (Tables 3.1-3.2, Figure 3.4). Post-hoc analyses indicated that all regions differed from each other, with Calgary being the most aggregated in both dispersal groups (Figure 3.2A-B). For the active dispersers, FL was more aggregated than MO, but this reversed for the passive dispersers (Figure 3.2A-B). Assembly treatment (drought versus control) significantly affected aggregation, with communities in drought tanks being more aggregated than those in control tanks (Figure 3.3) across both dispersal groups.

There was a significant interaction between assembly treatment and region, but this varied with active vs. passive dispersers. Missouri active dispersers were more aggregated in drought versus control treatment, while the reverse was true in Florida (Figure 3.4A, Table 3.1). Florida passive dispersers were significantly more aggregated in drought versus control treatment, but the other two regions showed no patterns of aggregation with treatment (Figure 3.4B, Table 3.2). Thus, the effect of environmental filtering on aggregation varied with latitude, but inconsistently across regions and dispersal groups resulting in varying effects sizes within regions and among dispersal groups (Table 3.3).

Because aggregation is a function of regional and local ENSpie, we further investigated how α -pie and γ -pie varied with region and treatment using a 2-way crossed ANOVA. For the active dispersers, γ -pie varied with region and community assembly treatment, and the effect of assembly varied with region as evidenced by a

significant interaction term (Table 3.4, Figure 3.5A). Also for the active dispersers, α -pie did not vary with region or assembly treatment, but there was a significant interaction term (Table 3.6, Figure 3.6A). Similarly, the passive dispersers showed significant main and interaction terms for γ -pie (Table 3.5, Figure 3.5B), but there were no significant main or interactive effects on α -pie (Table 3.7, Figure 3.6B). These results overall show that γ -pie is much more variable than α -pie. Furthermore, in response to the environmental filter, changes in γ -pie tend to drive significant changes in aggregation, as evidenced by every significant change in β -pie having the same directional change as γ -pie (Table 3.8).

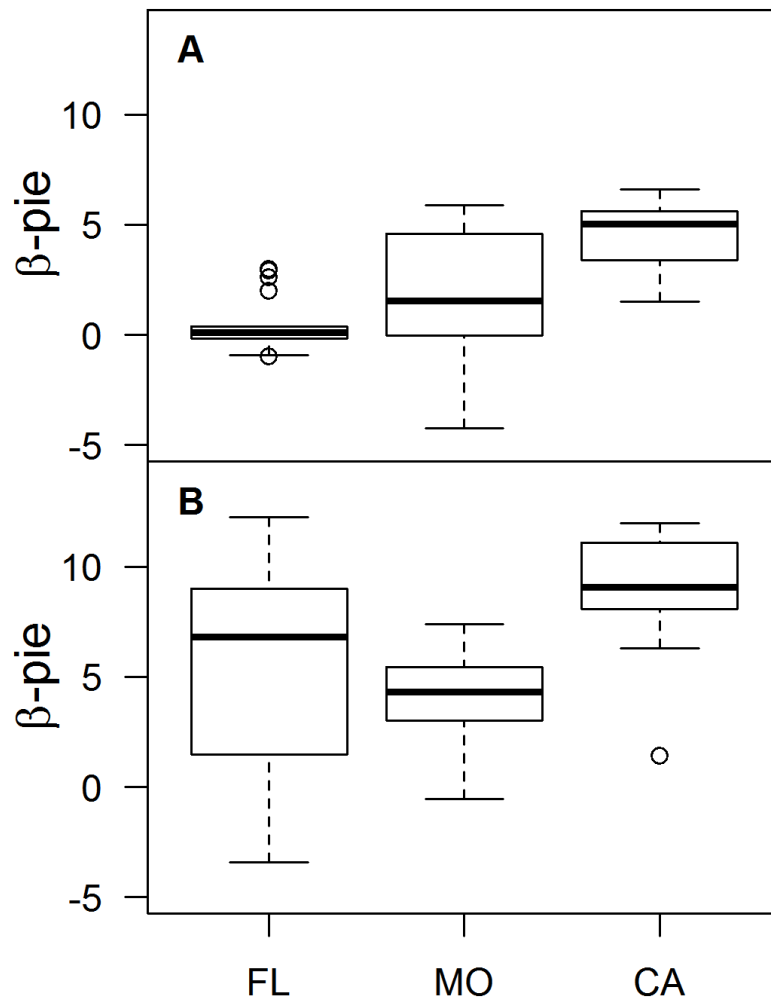


Figure 3.2. Main effect of region (FL = Orlando, Florida; MO = St. Louis, Missouri; CA = Calgary, Alberta, CA) on β -pie across both treatments for active (A) and passive (B) dispersers. Black lines are median values.

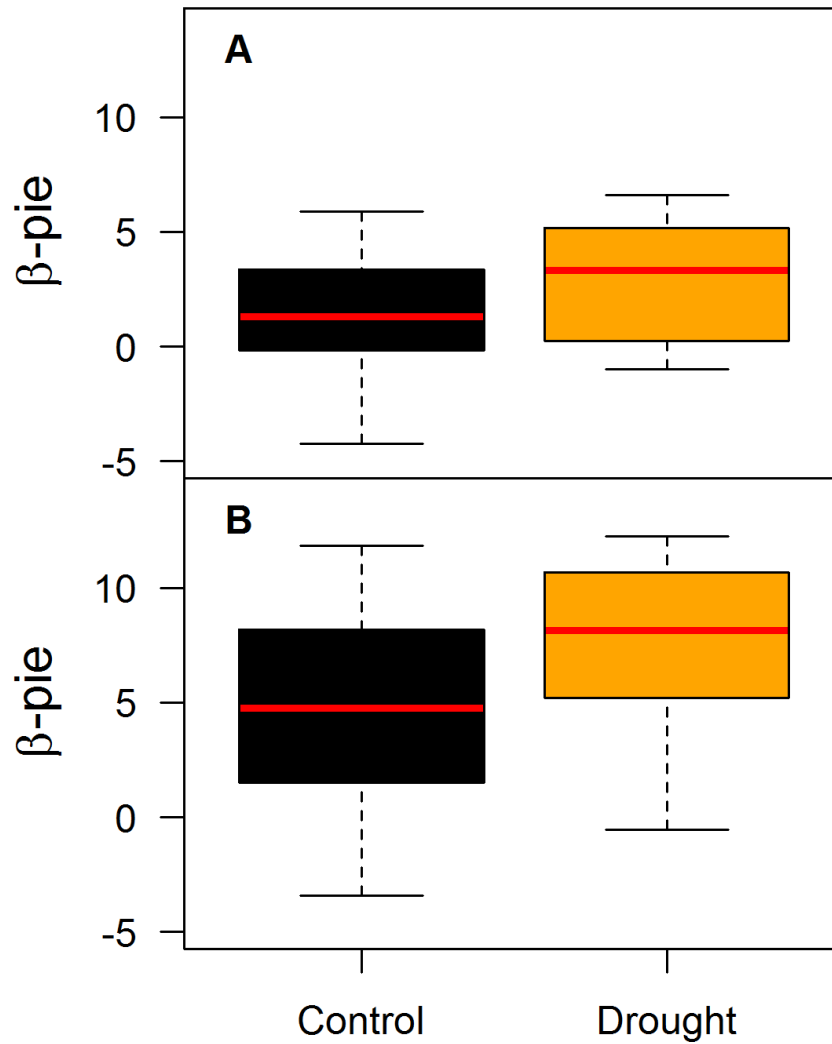


Figure 3.3. Main effect of treatment on β -pie across both treatments for active (A) and passive (B) dispersers. Red lines are median values.

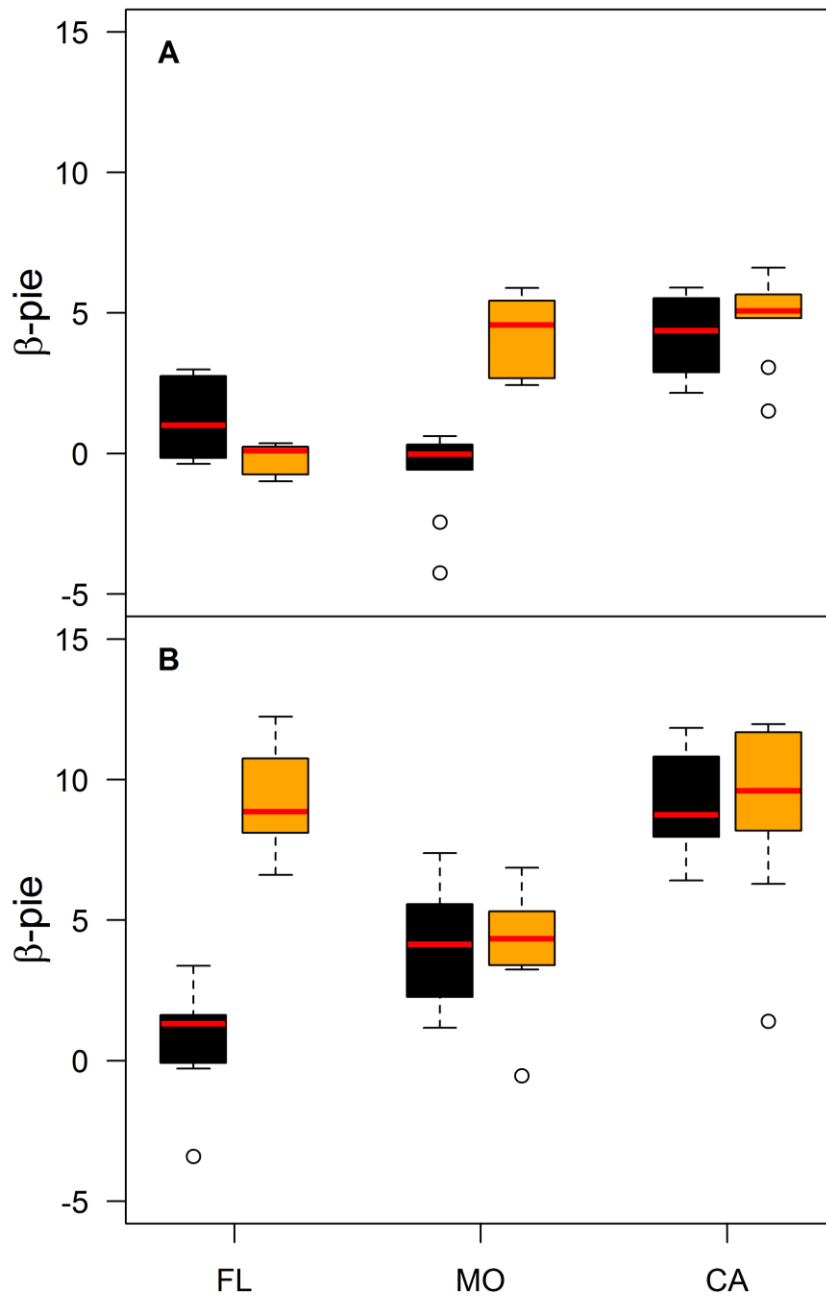


Figure 3.4. β -pie for (A) active and (B) passive dispersers in the drought (orange) and control (black) treatments across each region (FL = Orlando, Florida; MO = St. Louis, Missouri; CA=Calgary, Alberta, CA). Red lines are median values.

Table 3.1. (A) 2-way ANOVA table for the effect of region (FL, MO, CA) and assembly treatment (drought, control) on β -pie for active dispersers. (B) Planned contrasts for the main effect of region on aggregation (top three rows) and for each assembly treatment within each region (bottom three rows). Adjusted p-values obtained with Tukey's honest significance difference test.

A	df	SS	MS	F	p
Region	2	148.71	74.35	43.01	<0.001
Assembly	1	20.35	20.35	11.77	<0.01
Region:Assembly	2	118.37	59.18	34.24	<0.001
Residuals	54	93.34	1.73		

B	diff	lower	upper	p adj
FL-CA	-3.73	-4.73	-2.73	<0.001
MO-CA	-2.72	-3.72	-1.72	<0.001
MO-FL	1.01	0.01	2.01	0.05
FL:drought-FL:control	-1.88	-3.62	-0.15	0.03
MO:drought-MO:control	4.90	3.16	6.63	<0.001
CA:drought-CA:control	0.48	-1.25	2.22	0.96

Table 3.2. (A) 2-way ANOVA table for the effect of region (FL, MO, CA) and assembly treatment (drought, control) on β -pie for passive dispersers. (B) Planned contrasts for each assembly treatment within each region. Adjusted p-values obtained with Tukey's honest significance difference.

A	df	SS	MS	F	p
Region	2	271	135.5	28.26	<0.001
Assembly	1	106.1	106.1	22.14	<0.001
Region:Assembly	2	201.8	100.9	21.04	<0.001
Residuals	54	258.9	4.8		

B	diff	lower	upper	p adj
FL-CA	-3.70	-5.36	-2.03	<0.001
MO-CA	-5.02	-6.69	-3.35	<0.001
MO-FL	-1.33	-3.00	0.34	0.14
FL:drought-FL:control	7.84	4.95	10.73	<0.001
MO:drought-MO:control	0.28	-2.61	3.18	1
CA:drought-CA:control	-0.14	-3.04	2.75	1

Table 3.3. Effect size of the drought treatment on β -pie within each region (FL, MO, CA) for active and passive dispersers. Effect size is Cohen's d (margin of error of d).

	FL	MO	CA
Active	1.799 (0.933)	-3.381 (1.247)	-0.341 (0.782)
Passive	-4.22 (1.446)	-0.138 (0.777)	0.056 (0.775)

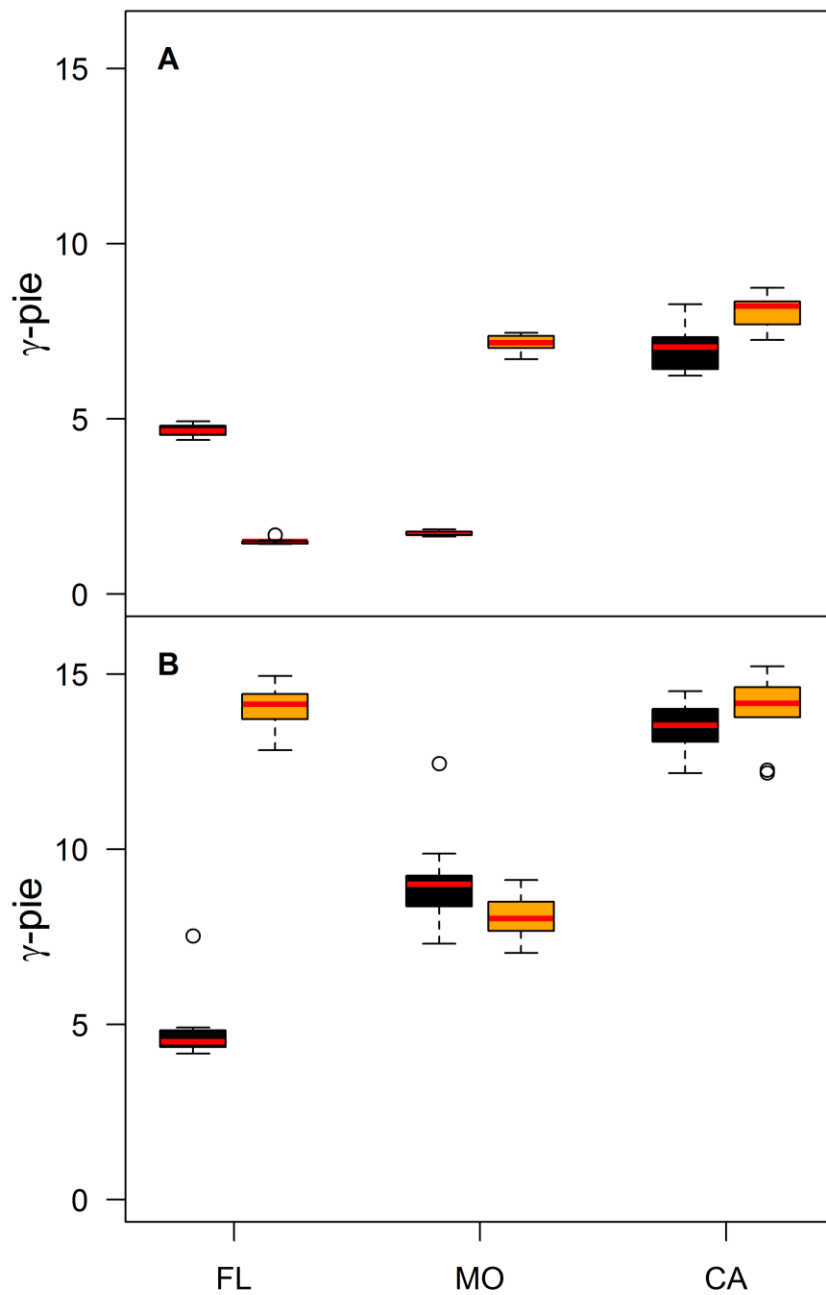


Figure 3.5. γ -pie for (A) active and (B) passive dispersers in the drought (orange) and control (black) treatments across each region (FL = Orlando, Florida; MO = St. Louis, Missouri; CA=Calgary, Alberta, CA). Red lines are median values.

Table 3.4. (A) 2-way ANOVA table for the effect of region (FL, MO, CA) and assembly treatment (drought, control) on γ -pie for active dispersers. (B) Planned contrasts for the main effect of region and for each assembly treatment within each region. Adjusted p-values obtained with Tukey's honest significance difference test.

A	df	SS	MS	F	p
Region	2	193.29	96.65	723.48	<0.001
Assembly	1	12.58	12.58	94.14	<0.001
Region:Assembly	2	208.55	104.28	780.60	<0.001
Residuals	54	7.21	0.13		

B	diff	lower	upper	p adj
FL-CA	-4.23	-4.51	-3.96	<0.001
MO-CA	-3.14	-3.42	-2.86	<0.001
MO-FL	1.09	0.82	1.37	<0.001
FL:drought-FL:control	-3.71	-4.19	-3.22	<0.001
MO:drought-MO:control	5.43	4.94	5.91	<0.001
CA:drought-CA:control	1.03	0.54	1.51	<0.001

Table 3.5. (A) 2-way ANOVA table for the effect of region (FL, MO, CA) and assembly treatment (drought, control) on γ -pie for passive dispersers. (B) Planned contrasts for each assembly treatment within each region. Adjusted p-values obtained with Tukey's honest significance difference.

A	df	SS	MS	F	p
Region	2	280.9	140.47	148.4	<0.001
Assembly	1	102.2	102.25	108.0	<0.001
Region:Assembly	2	256.2	128.10	135.4	<0.001
Residuals	54	51.1	0.95		

B	diff	lower	upper	p adj
FL-CA	-3.82	-4.56	-3.08	<0.001
MO-CA	-5.09	-5.83	-4.35	<0.001
MO-FL	-1.27	-2.01	-0.53	<0.001
FL:drought-FL:control	8.39	7.11	9.68	<0.001
MO:drought-MO:control	-1.02	-2.31	0.26	0.19
CA:drought-CA:control	0.46	-0.82	1.75	0.89

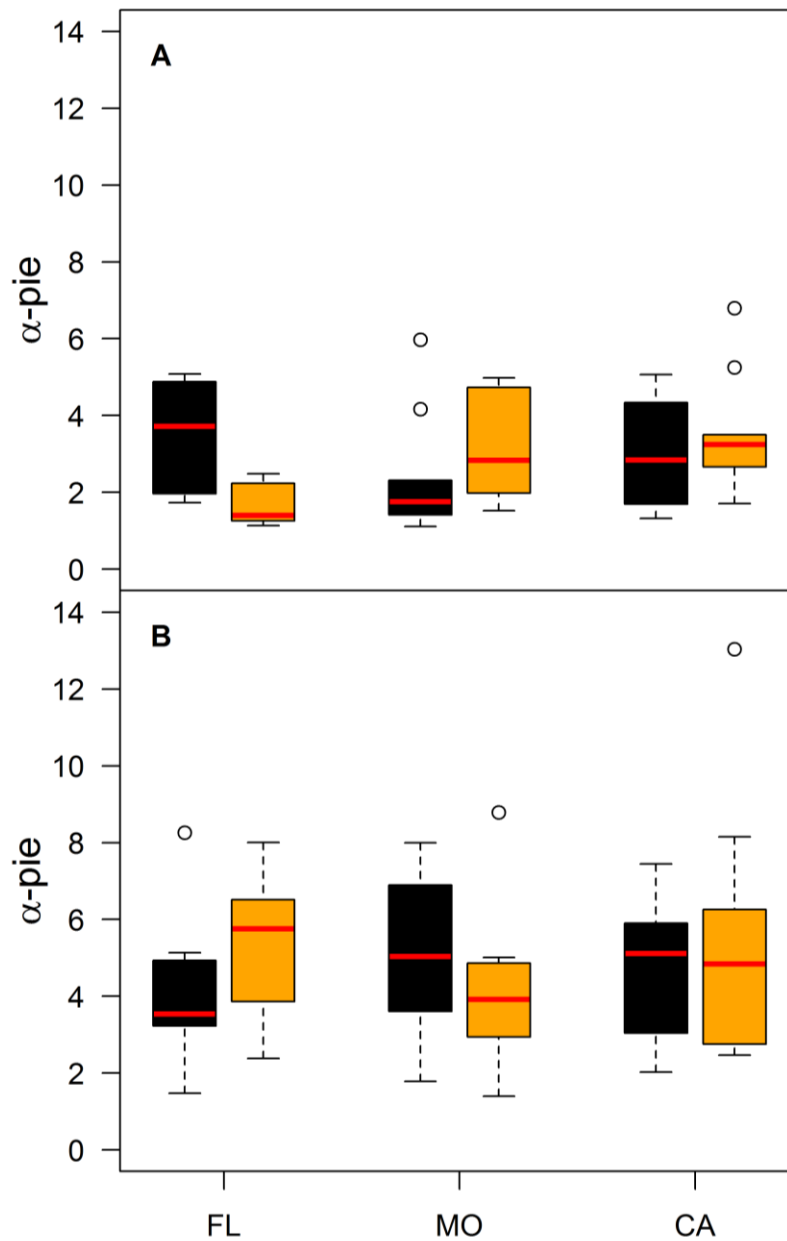


Figure 3.6. α -pie for (A) active and (B) passive dispersers in the drought (orange) and control (black) treatments across each region (FL = Orlando, Florida; MO = St. Louis, Missouri; CA=Calgary, Alberta, CA). Red lines are median values.

Table 3.6. (A) 2-way ANOVA table for the effect of region (FL, MO, CA) and assembly treatment (drought, control) on α -pie for active dispersers. (B) Planned contrasts for each assembly treatment within each region. Adjusted p-values obtained with Tukey's honest significance difference.

A	df	SS	MS	F	p
Region	2	4.81	2.407	1.393	0.26
Assembly	1	0.36	0.363	0.21	0.65
Region:Assembly	2	21.97	10.987	6.356	<0.01
Residuals	54	93.34	1.729		

B	diff	lower	upper	p adj
FL:drought-FL:control	-1.86	-3.60	-0.13	0.03
MO:drought-MO:control	0.78	-0.95	2.52	0.76
CA:drought-CA:control	0.61	-1.12	2.35	0.90

Table 3.7. 2-way ANOVA table for the effect of region (FL, MO, CA) and assembly treatment (drought, control) on α -pie for passive dispersers. No contrasts are shown because there were no significant region or interaction effects.

	df	SS	MS	F	p
Region	2	1.94	0.969	0.202	0.82
Assembly	1	0.77	0.772	0.161	0.69
Region:Assembly	2	15.74	7.872	1.642	0.20
Residuals	54	258.94	4.795		

Table 3.8. Directional change in ENSpie values at α -, β -, and γ -levels for the drought treatment relative to the controls. Up arrows indicate that ENSpie was larger in the drought than control treatment. Only cells with arrows indicate significant differences between treatments within that region. γ -pie values are for the jackknifed estimates.

	FL			MO			CA		
	α -pie	γ -pie	β -pie	α -pie	γ -pie	β -pie	α -pie	γ -pie	β -pie
Active Dispersers	↑	↓	↓	—	↑	↑	—	↓	—
Passive Dispersers	—	↑	↑	—	—	—	—	—	—

3.4 Discussion

In this experiment we aimed to standardize community histories, spatial layout, and an environmental filter to assess if there are consistent overall trends in the importance of an environmental filter – drought – in affecting intraspecific aggregation across three latitudes. There was a main trend of increased deterministic aggregation (and decreased stochasticity) with latitude (Figure 3.2), in which β -pie was highest in Calgary across both dispersal groups. There was also a significant main effect of drought, wherein communities were more aggregated after the drought compared to controls (Figure 3.3). However, there was no general pattern of the relative importance of environmental filtering with latitude, which resulted in a significant interaction between region and drought treatment for both dispersal groups (Tables 3.1-3.2). In fact, the environmental filter could either decrease (active dispersers, FL) or increase (active dispersers MO; passive dispersers, FL) aggregation (Figure 3.4). In addition, although either changes in α -pie, γ -pie, or both, can result in changes in β -pie, it appears that it is at the regional level where aggregation patterns manifest in response to the filtering treatment (Figures 3.5-3.6, Table 3.8). That is, drought has no effect on α -pie, but has a large effect on γ -pie that determines how β -pie is affected by the environmental filter.

The highest latitude site was significantly more aggregated than the other two sites across both dispersal groups. For the active dispersers, there was a consistent trend in aggregation across the three latitudes, with Missouri also being significantly more aggregated than Florida. Aggregation did not differ between Missouri and Florida sites for the passive dispersers, but they were significantly less aggregated than

Calgary. As β -pie deviates from zero, communities also deviate from spatial aggregation patterns expected due to stochastic sampling of individuals from the regional species pool. These results are thus consistent with the hypothesis that low latitude communities appear more stochastically assembled than high latitudes. However, as these are just static spatial patterns, more thorough investigations would need to be done to assess if other deterministic mechanisms are also affecting community assembly differentially with latitude. For example, stochastic assembly can occur simultaneously with deterministic species interactions, such as in the case with priority effects. During priority effects, initial colonization is stochastic with respect to species identities but early colonists deterministically prevent later invaders from establishment, creating alternative communities that are deterministically stable through time (alternative stable states) (Law and Morton 1993). However, there is little experimental evidence to support the prominence of priority effects, and it has alternatively been suggested that communities progress through alternative transient states in which communities vary both in space and time (Fukami and Nakajima 2011). Therefore, it is likely that the strength of this relationship between stochasticity and assembly may vary with taxonomic group, dispersal ability, or other aspects of regional species pools such as functional traits (e.g. ability to reproduce asexually or form dormant stages).

The effect of drought on aggregation did not vary consistently with latitude. For both dispersal groups, there was no difference in aggregation between the control and drought treatments at the highest latitude site (Table 3.8). This means that although aggregation levels were high in Alberta, Canada, drought communities had the same degree of non-stochastic interspecific clumping as the controls. This could indicate that

some other environmental filters were maintaining high spatial aggregation, irrespective of the drought filter, or that perhaps deterministic species interactions were very important.

For the other two sites, the effect of drought varied between the two dispersal groups. In Florida, the active dispersers were less aggregated and the passive dispersers were more aggregated in the drought treatment. In Missouri, there was no effect of drought for the active dispersers, but there was an increase in aggregation for the passive dispersers. Although there was a slight decrease in aggregation for Florida active dispersers, there were much greater and positive effects on aggregation for the other two significant site x treatment effects. This was somewhat surprising because Chase's mesocosm experiment in Pennsylvania (2007), comparing drought versus control treatments and measuring β -diversity, found the opposite effect across both zooplankton and macroinvertebrates. In fact, a common expectation for the effect of disturbance on β -diversity is that it tends to homogenize communities rather than aggregate them (Chase 2007, Vellend et al. 2007, Vanschoenwinkel et al. 2013, Lopes et al. 2014). Theoretically this is because only a subset of species can tolerate the disturbance, leading to less variation in community composition (Olden 2006, Olden and Rooney 2006, Balata et al. 2007, Ross et al. 2012, Magurran et al. 2015). Alternatively, and more likely here, the environmental filter can increase aggregation if it eliminates the regionally dominant competitors, allowing for the emergence of otherwise spatially aggregated and outcompeted rare species (Petraitis et al. 1989, Svensson et al. 2012, Velle et al. 2014, Stubbington et al. 2015).

Finally, one of the more consistent patterns of this experiment is that significant effects of drought on aggregation appear to be driven by changes at the regional (treatment), not local (mesocosm), level. That is, on average, α -pie, or evenness, of a mesocosm did not differ between drought and control treatments. Instead, if β -pie significantly varied between treatments, it was matched by a concomitant change in γ -pie. When aggregation increased, this indicates that although local evenness stayed the same, the dominant species in each tank tended to differ in the drought tanks. In other words, species that were regionally abundant in the control tanks became much less so in the drought treatment, which is consistent with the idea that disturbance can increase aggregation by decreasing regionally abundant dominant species. This result emphasizes the perspective that regional-level processes can have large impacts on local communities (Ricklefs 1987) and that it is the interaction among different types of processes, such as environmental filtering with deterministic species interactions, that shape community composition.

3.5 References

- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* **10**:95-104.
- Alonso, D., R. S. Etienne, and A. J. McKane. 2006. The merits of neutral theory. *Trends in Ecology & Evolution* **21**:451-457.
- Balata, D., L. Piazzzi, and L. Benedetti-Cecchi. 2007. Sediment disturbance and loss of beta diversity on subtidal rocky reefs. *Ecology* **88**:2455-2461.
- Bell, G. 2001. Neutral Macroecology. *Science* **293**:2413-2418.
- Bray, J. and J. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27**:325-349.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* **104**:17430-17434.
- Chase, J. M. 2010. Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science* **328**:1388-1391.
- Chase, J. M. and T. M. Knight. 2013. Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters* **16**:17-26.
- Chase, J. M. and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **366**:2351-2363.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* **7**:241-253.

- Dauby, G. and O. J. Hardy. 2012. Sampled-based estimation of diversity sensu stricto by transforming Hurlbert diversities into effective number of species. *Ecography* **35**:661-672.
- Dobzhansky, T. 1950. Evolution in the Tropics. *American Scientist* **38**:209-221.
- Fischer, A. G. 1960. Latitudinal variations in organic diversity. *Evolution* **14**:64-81.
- Fukami, T. and M. Nakajima. 2011. Community assembly: alternative stable states or alternative transient states? *Ecology Letters* **14**:973-984.
- Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients *Annals of the Missouri Botanical Garden* **75**:1-34.
- Gotelli, N.J. and A.M. Ellison. 2004. *A Primer of Ecological Statistics*. Sinauer Associates, Inc., Sunderland, MA.
- Hubbell, S. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton, NJ.
- Hurlbert, S.H., 1971, The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, v. 52, p. 577-586. (On explicit calculation of rarefaction richness and derivation of Hurlbert's PIE measure of evenness.)
- Jost, L. 2006. Entropy and diversity. *Oikos* **113**:363-375.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* **88**:2427-2439.
- Keddy, P. A. 1992. Assembly and Response Rules - 2 Goals for Predictive Community Ecology. *Journal of Vegetation Science* **3**:157-164.

- Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science* **333**:1755-1758.
- Lande, R., P. J. DeVries, and T. R. Walla. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos* **89**:601-605.
- Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**:545-556.
- Law, R. and R. D. Morton. 1993. Alternative permanent states of ecological communities. *Ecology* **74**:1347-1361.
- Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing Beta Diversity: Partitioning the Spatial Variation of Community Composition Data. *Ecological Monographs* **75**:435-450.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**:601-613.
- Lopes, P. M., L. M. Bini, S. A. J. Declerck, V. F. Farjalla, L. C. G. Vieira, C. C. Bonecker, F. A. Lansac-Toha, F. A. Esteves, and R. L. Bozelli. 2014. Correlates of Zooplankton Beta Diversity in Tropical Lake Systems. *Plos One* **9**.

- MacArthur, R. and E. Wilson. 1963. An equilibrium theory of insular zoogeography
Evolution **17**:373-387.
- Magurran, A. E., M. Dornelas, F. Moyes, N. J. Gotelli, and B. McGill. 2015. Rapid biotic
homogenization of marine fish assemblages. Nature Communications **6**.
- Matthews, T. J. and R. J. Whittaker. 2014. Neutral theory and the species abundance
distribution: recent developments and prospects for unifying niche and neutral
perspectives. Ecology and Evolution **4**:2263-2277.
- McGill, B. J. 2010. Towards a unification of unified theories of biodiversity. Ecology
Letters **13**:627-642.
- McIntosh, M. S. 1983. Analysis of combined experiments. Agronomy Journal **75**: 153–
155.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush,
S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R.
McCune, L. A. McDade, M. A. McPeck, T. J. Near, T. D. Price, R. E. Ricklefs, K.
Roy, D. F. Sax, D. Schluter, J. M. Sobel, and M. Turelli. 2007. Evolution and the
latitudinal diversity gradient: speciation, extinction and biogeography. Ecology
Letters **10**:315-331.
- Mori, A. S., S. Fujii, R. Kitagawa, and D. Koide. 2015. Null model approaches to
evaluating the relative role of different assembly processes in shaping ecological
communities. Oecologia **178**:261-273.
- Myers, J. A., J. M. Chase, I. Jimenez, P. M. Jorgensen, A. Araujo-Murakami, N.
Paniagua-Zambrana, and R. Seidel. 2013. Beta-diversity in temperate and

- tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters* **16**:151-157.
- Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* **33**:2027-2039.
- Olden, J. D. and T. P. Rooney. 2006. On defining and quantifying biotic homogenization. *Global Ecology and Biogeography* **15**:113-120.
- Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* **104**:377-387.
- Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The Maintenance of Species-Diversity by Disturbance. *Quarterly Review of Biology* **64**:393-418.
- Pianka, E. R. 1966. Latitudinal Gradients in Species Diversity: A Review of Concepts. *The American Naturalist* **100**:33-46.
- Qian, H., C. Badgley, and D. L. Fox. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography* **18**:111-122.
- Qian, H. and R. E. Ricklefs. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography* **21**:341-351.
- Qian, H. and J. S. Song. 2013. Latitudinal gradients of associations between beta and gamma diversity of trees in forest communities in the New World. *Journal of Plant Ecology* **6**:12-18.

- Qiao, X., F. Jabot, Z. Tang, M. Jiang, and J. Fang. 2015. A latitudinal gradient in tree community assembly processes evidenced in Chinese forests. *Global Ecology and Biogeography* **24**:314-323.
- Ricklefs, R. E. 1987. Community diversity - relative roles of local and regional processes. *Science* **235**:167-171.
- Rosindell, J., S. P. Hubbell, and R. S. Etienne. 2011. The Unified Neutral Theory of Biodiversity and Biogeography at Age Ten. *Trends in Ecology & Evolution* **26**:340-348.
- Ross, L. C., S. J. Woodin, A. J. Hester, D. B. A. Thompson, and H. J. B. Birks. 2012. Biotic homogenization of upland vegetation: patterns and drivers at multiple spatial scales over five decades. *Journal of Vegetation Science* **23**:755-770.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is There a Latitudinal Gradient in the Importance of Biotic Interactions? *Annual Review of Ecology, Evolution, and Systematics* **40**:245-269.
- Stubbington, R., A. J. Boulton, S. Little, and P. J. Wood. 2015. Changes in invertebrate assemblage composition in benthic and hyporheic zones during a severe suprasedasonal drought. *Freshwater Science* **34**:344-354.
- Svensson, J. R., M. Lindegarth, P. R. Jonsson, and H. Pavia. 2012. Disturbance-diversity models: what do they really predict and how are they tested? *Proceedings of the Royal Society B-Biological Sciences* **279**:2163-2170.
- Tucker, C. M., L. G. Shoemaker, K. F. Davies, D. R. Nemergut, and B. A. Melbourne. 2016. Differentiating between niche and neutral assembly in metacommunities using null models of beta-diversity. *Oikos* **125**:778-789.

- Tuomisto, H. 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* **33**:2-22.
- Tuomisto, H. 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* **33**:23-45.
- Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodriguez. 1995. Dissecting Amazonian biodiversity *Science* **269**:63-66.
- Vanschoenwinkel, B., F. Buschke, and L. Brendonck. 2013. Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. *Ecology* **94**:2547-2557.
- Velle, L. G., L. S. Nilsen, A. Norderhaug, and V. Vandvik. 2014. Does prescribed burning result in biotic homogenization of coastal heathlands? *Global Change Biology* **20**:1429-1440.
- Vellend, M., K. Verheyen, K. M. Flinn, H. Jacquemyn, A. Kolb, H. Van Calster, G. Peterken, B. J. Graae, J. Bellemare, O. Honnay, J. Brunet, M. Wulf, F. Gerhardt, and M. Hermy. 2007. Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *Journal of Ecology* **95**:565-573.
- Vellend, M., D. S. Srivastava, K. M. Anderson, C. D. Brown, J. E. Jankowski, E. J. Kleynhans, N. J. B. Kraft, A. D. Letaw, A. A. M. Macdonald, J. E. Maclean, I. H. Myers-Smith, A. R. Norris, and X. X. Xue. 2014. Assessing the relative

- importance of neutral stochasticity in ecological communities. *Oikos* **123**:1420-1430.
- Wallace, A. R. 1878. *Tropical Nature and Other Essays*. Macmillan, New York.
- Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and S. Bentivenga. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B-Biological Sciences* **366**:2403-2413.
- Whittaker, R. 1956. *Vegetation of the Great Smoky Mountains*. *Ecological Monographs* **26**:1-60.
- Xu, W. B., G. K. Chen, C. R. Liu, and K. P. Ma. 2015. Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Global Ecology and Biogeography* **24**:1170-1180.

Chapter 4: The effect of dispersal on aggregation varies with latitude, the stage of community assembly, and taxonomic group

4.1 Introduction

Dispersal plays a fundamental role in the establishment and maintenance of ecological communities. At the local scale, there is abundant evidence across a wide range of taxa and ecosystems that species richness increases with dispersal from the species pool (Tilman 1997, Cadotte 2006, Lee and Bruno 2009, Myers and Harms 2009). In addition to affecting the composition of single communities, dispersal also affects our expectations about compositional differences among communities, generally termed β -diversity. In general, experimental work shows that dispersal tends to reduce β -diversity (Cadotte 2006), which has also been found in theoretical work (Mouquet and Loreau 2003), as well as in observational studies that take advantage of organisms' differential dispersal abilities (Qian 2009, Gómez-Rodríguez et al. 2015). However, β -diversity also can increase with dispersal, for example when new heterogeneity is introduced into a landscape through disturbance (Questad and Foster 2008, Vanschoenwinkel et al. 2013), or when there is a high correlation between dispersal and fitness in a heterogeneous landscape (Vellend et al. 2014). This latter scenario is related to the metacommunity concept of species sorting, in which species disperse among local communities, with β -diversity arising due to the deterministic filters of different patches (Leibold et al. 2004).

Although it is commonly acknowledged that both biotic and abiotic factors, along with dispersal, affect the assembly of ecological communities, much community assembly work focuses on abiotically and spatially driven change in community composition (Qian and Ricklefs 2012, Wang et al. 2012, Myers et al. 2013).

Theoretically species should also sort along biotic gradients when species interactions affect colonization ability or community co-occurrence (Levins and Culver 1971, Law and Morton 1996, Holt and Polis 1997, Mouquet and Loreau 2002). In addition, even if abiotic and biotic environments are suitable, stochasticity and historical contingency can play a large role in whether or not dispersal results in successful colonization.

Demographic stochasticity is especially important when population sizes are small, such that it could affect species that typically disperse as individuals or in small populations (Lande et al. 2003, Orrock and Fletcher 2005). If stochasticity affects the order in which species successfully colonize communities, then any biotic interactions between late dispersers and already established species in a community could either promote or hinder further colonization events. The potential importance of the interaction between deterministic species interactions and stochastic processes in community assembly was emphasized by Law and Morton (1993) in what is generally termed priority effects. In priority effects, colonization is stochastic with respect to species identity, but early colonists are able to deterministically prevent later dispersers from establishment. The result is alternative communities, i.e. non-zero spatial β -diversity, that are stable through time, despite having identical abiotic environments. More recently Fukami and Nakajima (2011) also emphasized the importance of historical contingency in dispersal, but suggested that more often

communities might be alternative transient states, highlighting that very abiotically similar communities can vary in both space and time. Nevertheless, both stochastic and deterministic processes, and their interaction with dispersal, likely affect all communities, and the question remains if there are any general trends in the relative importance of these factors across biogeographical gradients (Chase and Myers 2011).

How communities may be differentially regulated across latitudes has been of longstanding interest in ecology. For example, as early as Wallace (1878) ecologists have conjectured that the importance of biotic interactions might vary with latitude. Although varied in nuance, most explanations for a latitudinal gradient in the importance of species interactions emphasize the opposite gradient in environmental harshness; only the more stable and benign low latitude environments allow for the evolution of intense, specialized biotic interactions (Schemske et al. 2009). More recently, contrasting ideas about the direction of the biotic-latitudinal gradient have emerged, partly due to Hubbell's neutral theory of biodiversity. In particular, it has been suggested that perhaps high diversity, low latitude communities consist of more "neutral" species that may differ ecologically but are essentially (or nearly so) equivalent in their effects on each other (Hubbell 2006). As neutral species are affected purely by stochasticity and dispersal limitation rather than deterministic species interactions, under this scenario, the role of species interactions in community assembly would actually tend to increase and stochasticity would tend to decrease with latitude.

Here, we investigate the effect of the interaction of dispersal, stochastic, and deterministic assembly processes in an outdoor mesocosm experiment replicated

across three latitudes in North America: Orlando, FL (28°N); St Louis, MO (39°N); and Calgary, AB, Canada (51°N). By using mesocosms, we greatly reduced within-latitude abiotic gradients and historical effects in driving within-latitude β -diversity, thus focusing on the interaction of dispersal, biotic interactions, and stochasticity. Finally, we investigated these interactions at two different times in the assembly process: 1) at the initial inoculation of the communities, and 2) two years after the communities were initially assembled. These two dispersal treatments allowed us to assess if the magnitude of dispersal at different times in assembly alters community composition, and if the relative importance of that dispersal varies with latitude.

For the first dispersal treatment, we focus on initial assembly, when successful colonization of species is often greatly influenced by stochasticity due to small colonizing population sizes (Lande et al. 2003). From a purely probabilistic perspective, demographic stochasticity should play a smaller role and deterministic species interactions a larger role in affecting community composition when propagule pressure is relatively high. Under this scenario, we hypothesize that the high early dispersal treatment will tend to homogenize communities, resulting in comparatively low β -diversity. If initial propagule pressure is not important in community assembly, such as if the same good colonizers are always successful, then there should be no difference in β -diversity between these treatments.

Finally, if the relative importance of initial propagule pressure varies with latitude, then the relative effect of this treatment (within region treatment effect size on β -diversity) should vary systematically across these three latitudes. If the relative importance of initial propagule pressure increases with latitude, then the effect size will

also tend to increase with latitude. Alternatively, if the relative importance of initial propagule pressure decreases with latitude, then the opposite trend should occur.

The second dispersal treatment was aimed at assessing the importance of dispersal in affecting community composition after relatively complete communities have been assembled. We expect that increased dispersal will provide greater opportunity for species to interact, thus playing a larger role in regulating community composition. Based on theoretical, observational, and experimental research (Mouquet and Loreau 2003, Cadotte 2006, Logue et al. 2011), we hypothesize that dispersal should tend to homogenize communities, thus decreasing β -diversity, within a region. Alternatively, dispersal could cause species sorting along biotic (or abiotic) gradients, resulting in higher β -diversity within a region (e.g. Questad and Foster 2008, Vanschoenwinkel et al. 2013). Further, in the case of perfect priority effects, we expect no effect of dispersal on β -diversity.

Finally, if the relative importance of dispersal late in assembly varies with latitude, then the relative effect of this treatment will vary systematically across these three latitudes. If, for example, dispersal limitation increases with latitude, then the effect size of aggregation will also increase with latitude. The opposite trend would suggest that communities at low latitudes are less dispersal limited.

4.2 Methods

4.2.1 Establishment

From March-June 2011, 30 outdoor mesocosms (2365-L cattle tanks) were established at each of three locations spanning 23 degrees latitude in North America (Figure 4.1): Orlando, FL, USA (28°N); St Louis, MO, USA (39°N); and Calgary, AB, Canada (51°N). The mesocosms simulated small pond communities, receiving inocula of aquatic species, as well as being open to colonization from more mobile aquatic dispersers. To establish communities, the mesocosms initially received 5 cm of topsoil and were filled with well water before inoculation. Both the soil and water originated from the region of the experimental location, which served to preserve some of the environmental conditions of each region. The topsoil provided nutrients for primary productivity and substrate for macrophyte root systems. After soil and water addition, aquatic producers and consumers were collected from 15 ponds within a 25 km radius of the experimental site. For each of the 15 ponds, plankton were collected from the water column by filtering 10L of water through a 80 µm net. Because many aquatic species are seasonal and form dormant stages, approximately 38L (10 gallons) of sediments was also collected from each pond. Finally, 9 species of macrophytes were collected across all 15 ponds, which were chosen due to their relatively high abundance, their known ability to survive in outdoor mesocosms, or because they inhabited shallow depths and thus had a greater chance to survive in our experimental ponds. The macrophytes were transported back to the experimental site in pond water to ensure their viability, which included additional small invertebrates from which we

could inoculate the experimental ponds. All the collected water and pond sediments (and the organisms/resting stages contained in them) were combined in separate slurries, which were the initial inocula of the experimental ponds for each region. Because of their size and biology, the macrophytes were added individually so as to ensure the same number of individuals per species reached each mesocosm.

4.2.2 Dispersal Treatments

There were three dispersal treatments with ten replicates each (3 x 10=30 tanks per site) used to perform two experiments. The first experiment focused on how initial propagule pressure affects community assembly. In this experiment the control and treatment mesocosms (heretofore referred to as extra initial biomass, or EIB) differed in the total volume or number of individuals of inocula added to the mesocosms during the initial establishment of the mesocosm communities. The control mesocosms received 2-3 individuals of each macrophyte species, 2L of sediments, 50mL of concentrated plankton, and 250mL of invertebrates larger than 80 μm . The extra initial biomass treatment received 3-10x that amount of the same slurries: 6-10 individuals of each macrophyte species, 20L of sediments, 500 mL of plankton, and 1L of large invertebrates. Because organic matter provides nutrients for aquatic communities and can affect water chemistry, we added the same amount of dead organisms/sediment from the extra biomass treatment to the control. The macrophytes were dried for 3 days in direct sunlight, followed by soaking in 95% ethanol before being added to the

control mesocosms. Slurry water of invertebrates was boiled for 20 minutes, and to account for the extra sediment, we added 18L of topsoil to the control tanks.

The inoculation of more individuals in the extra biomass mesocosms aimed to decrease the role of stochasticity and increase the probability of deterministic species interactions in affecting community composition during the initial establishment of aquatic communities. This expectation is based solely on the fact that the role of stochasticity increases as population size decreases (Lande et al. 2003, Orrock and Fletcher 2005). Thus, if species interactions or traits affect colonization and community assembly, then the extra initial biomass treatments would show more non-random β -diversity patterns relative to the control. If this varies with latitude, then the effect of the extra initial biomass treatment on β -diversity relative to the control treatment should vary among regions.

The second experiment investigated how dispersal later in assembly affects compositional variation in communities. It included the control mesocosms, as well as ten treatment mesocosms that were initially assembled identically to the control treatment. However, after two years, the ten treatment mesocosms received a dispersal treatment meant to homogenize (i.e. increase compositional similarity) those communities. The controls were left undisturbed.

The homogenization treatment was employed differently for two different groups of the aquatic community: zooplankton and lentic macroinvertebrates. For the zooplankton 5% of the community in each of the ten treatment mesocosms was removed. This required calculating each mesocosm's total water volume and then removing and filtering 5% of the total water volume through an 80 μ m net. For the lentic

macroinvertebrates, we removed ~50% of the community from each treatment mesocosm. This was done by first inserting a 1mm mesh window-screen barrier that bisected the mesocosm. The screen allowed for water and planktonic organisms to pass between the two sides, but restricted the movement of macroinvertebrates. The top and bottom of the screen were attached to PVC which allowed us to secure the placement of the screen barrier during the macroinvertebrate removal. The PVC on the bottom of the barrier was heavily weighted to keep it submerged in the sediment, and the PVC at the top was clamped to the edge of the mesocosm. With the screen halving the length of the mesocosm, D-nets (1 mm mesh) were used to remove all macroinvertebrates found in the water column of one-half of the mesocosm. To maintain the macrophyte communities and limit substrate disturbance during this process, we did not collect sediments or macrophytes; any accidentally removed macrophytes were rinsed and returned to the mesocosm. D-net sweeps were performed until three consecutive empty sweeps were achieved. To control for the disturbance of this treatment, D-net sweeps were also performed in the control mesocosms, using the homogenization treatment's average number of sweeps per region/latitude. All organisms caught during these control sweeps were returned to their incumbent mesocosm.

All zooplankton and invertebrate individuals removed from each homogenization tank were then combined into a single homogenized slurry. Equal portions of the slurry were dispersed back into those same mesocosms, giving each individual in the slurry an equal probability of being added back to each of the ten mesocosms. This slurry thus also represents the regional species abundance distribution, and the treatment

itself represents random (or nearly so) dispersal from that pool. As such, the homogenization treatment ultimately aimed to decrease β -diversity, as is expected by random dispersal and is commonly seen in metacommunity experiments (Cadotte 2006). Of additional interest was to determine the degree to which resident communities in the homogenization treatment could non-randomly prevent (or facilitate) the colonization of introduced species/individuals. For example, if community assembly is completely stochastic, then the homogenization treatment should lower β -diversity. However, if species are able to prevent later dispersers from colonizing, as in priority effects, then β -diversity in the homogenization treatment should be maintained and similar to the controls. Therefore, if the relative effect of homogenization on β -diversity varies with latitude, so does the relative importance of non-random processes, such as biotic interactions.

4.2.3 Sampling

All treatments across all sites were sampled for macrophytes, zooplankton, and macroinvertebrates from 2012-2014. Sampling was performed in March for Florida, USA; June for Missouri, USA; and July for Alberta, Canada to correspond to yearly increments after initial establishment. Macrophyte species were sampled non-destructively as the average of two percent-cover estimates. For estimates 10% or more, this was estimated to the nearest 5% increment; under 10% was to the nearest 1% increment. Zooplankton and macroinvertebrates were sampled destructively for identification and enumerated in the laboratory using compound and dissecting

microscopes, respectively. 5L of water per mesocosm was filtered through a 80 μm net, and the filtered zooplanktons were preserved in an acid-Lugols solution. Two hollow cylinders (0.36-m diameter x 1-m tall) were used to sample the macroinvertebrates communities of each mesocosm. Securing the bottom of the cylinders in benthic sediments restricted the loss of invertebrates, allowing for standardized sampling volumes among all mesocosms. Within the cylinders, invertebrates were found and extracted using dip nets (0.33 mm mesh) until 5 consecutive empty net sweeps was achieved. Any vertebrates found during the survey were identified and counted before being returned to the mesocosm. The invertebrates were preserved in 70% ethanol.

4.2.4 Quantifying β -diversity

β -diversity was measured as the additive difference between each mesocosm's (local, α) diversity and the treatment-wide (regional, γ) diversity at each site/latitude. The specific metric used was a modified version of Hurlbert's (1971) probability of interspecific encounter (PIE), which calculates the probability of selecting different species given two random samples from the same species abundance distribution (SAD). PIE thus increases with species diversity/evenness, and PIE is in fact the complement of the more widely used Simpson's diversity index D ($\text{PIE} = 1 - D$).

One of the useful properties of PIE is that it represents the initial slope of a rarefaction curve, which makes it relatively insensitive to the number of individuals sampled in a community or region (Olszewski 2004, Dauby and Hardy 2012). Thus as

PIE values increase, new species are encountered at a faster rate, and evenness/diversity increases. This also means that PIE is mostly sensitive to the abundant species, such that missed rare species do not yield misleading PIE values.

PIE values were thus calculated at the regional/treatment level as well as the local/mesocosm scale, which were then converted to an effective number of species (ENSpie; γ -pie and α -pie, respectively). ENSpie ($\text{ENSpie} = 1 / \sum_{i=1}^S p_i^2$, where S is the number of species in a community, and p_i is the relative abundance of species i) reflects how many equally abundant species there would be in a sample to reach an equivalent diversity value. Conversion of PIE to an effective number of species is necessary when comparing values across distributions that vary in sampling effort (i.e. number of individuals) (Jost 2006). The difference between the ENSpie of the region/treatment (γ -pie) and each local mesocosm (α -pie) then yielded a β -diversity value for each mesocosm at a single site within a treatment: $\beta\text{-pie} = \gamma\text{-pie} - \alpha\text{-pie}$.

This metric of β -diversity was selected because it is relatively insensitive to the size or shape of the regional/treatment SAD or to the number of individuals sampled locally (Olszewski 2004, Dauby and Hardy 2012). Simulations by Chase & Knight (2013) also show that α -pie values only vary when local communities are assembled non-stochastically from the regional pool. Since α -pie values are insensitive to the size or shape of the regional pool (γ -pie), then as β -pie deviates from zero, communities appear less stochastically assembled. Because of these aforementioned properties, β -pie also obviates the need for null modeling to account for such numerical sampling effects relating α - and γ -diversity to β -diversity. That is, non-zero β -pie values reflect the gain (or loss) of species when scaling from a single community to the regional, or

treatment, species pool, irrespective of the number of individuals sampled or the size and shape of the regional SAD. For clarity and ease, we will henceforth term this aspect of β -diversity (β -pie) as *aggregation*.

4.2.5 Analyses

Initial Establishment:

To assess how initial inocula volume/size affects community assembly, we compared aggregation of the extra biomass and control treatments using linear mixed models; region, dispersal treatment, and time were fixed effects and tank identification was the random effect sampled annually from 2012-2014. Often in repeated measures designs, samples taken closer in time will be more similar (have lower variance) to those taken farther apart in time, such that the appropriate variance-covariance structure must be specified in the model (Scheiner and Gurevitch 2001). The variance-covariance structure is referring to the variance between subjects (mesocosms) and the covariance between the same subjects at multiple points in time. For the macrophytes and zooplankton mixed models we fit the following structure types to each dataset separately: compound symmetry, unstructured, autoregressive, and autoregressive heterogeneous variances. We then assessed the best model fit using Akaike's Information Criteria (AIC) on each of the four models. When there was no significant differences between the two best fit ($\Delta AIC < 2$), we chose the model with the lowest AIC value. After the best fit variance-covariance structure was identified, we specified it in the full mixed model using the function `gls` in the `nlme` package in R. The `gls` function

uses generalized least squares to fit linear models and allows errors in the model to be correlated and/or have unequal variances. It also allows for unbalanced data, which was appropriate here because one of the tanks at the Missouri site was accidentally drained in the final year of the experiment.

We were specifically interested in the main effect and direction of the dispersal treatment, with the expectation that increased initial inocula decreases stochasticity and thus decreases aggregation relative to the control. When significant main effects for region or dispersal treatment or their interaction were found, post-hoc contrasts were performed. Any interactive effects of latitude/region with dispersal treatment would indicate if the effect of initial propagule pressure on aggregation varies with latitude. For example, if ecological equivalence decreases with latitude, then the difference between the control and extra initial biomass treatment would increase with latitude across our three sites. Separate analyses were done for macrophytes and zooplankton due to their differences in biomass and sampling methods. Macroinvertebrates were not analyzed because they vary in their ability to form dormant stages and we were therefore not confident of their manipulation during initial assembly. To directly quantify the effect of the treatment relative to controls, we also calculated an effect size measured as

Cohen's d : $d = \frac{M_1 - M_2}{SD_{pooled}}$, where M_1 and M_2 are the mean β -pie of the control and

dispersal treatments, respectively, and the denominator is the pooled standard deviation across both treatments.

Two Years Post Establishment:

To assess how within-region dispersal affects community assembly after two years, we quantified α -pie, β -pie, and γ -pie across for the control and homogenization treatments using the census data from 2014 only (the year after homogenization was imposed). As mentioned above, in 2014 one of the mesocosms in Missouri was accidentally drained prior to sampling, yielding an unbalanced design. As we were interested in both the main effects of region and the dispersal treatments, as well as their interaction, we performed a two-factor linear model using Type I sum of squares. Type I sum of squares with unbalanced data, however, will yield varying quantitative results depending on the order in which each main effect is considered. Therefore, for each taxonomic group, we performed two models that varied in the order of the two main effects to assess if there were any qualitative differences in the significance of each factor.

For the main effect of the dispersal treatment on aggregation, the expectation was that, in the absence of deterministic processes, increased among-community dispersal will homogenize communities compositionally, thus decreasing aggregation. We were also interested in the interaction between dispersal and latitude/region. If biotic filtering varies with latitude, then the effect of the homogenization treatment relative to controls should also vary with latitude. For example, a reverse latitudinal gradient in ecological equivalence (species are more equivalent at low latitudes) would result in smaller effects of the homogenization treatment relative to control as latitude decreases. This analysis was done separately for the lentic macroinvertebrates and zooplankton due to their differences in dispersal treatment (5% of the zooplankton versus 50% of the

macroinvertebrate individuals were dispersed) and sampling method. Macrophytes were not analyzed because they were not manipulated in the homogenization treatment. Direct comparison of the homogenization relative to controls was quantified using Cohen's *d*.

Due to unexpected effects of the dispersal treatment on aggregation patterns of the zooplankton communities, we further investigated how α -pie and γ -pie varied with region and treatment. For α -pie, this was done with the same two-factor linear model using Type I sum of squares as described for the aggregation analysis. Because only one γ -pie value was available per treatment and region combination, we first generated ten estimates of γ -pie to allow for statistical analysis with γ -pie estimates being the response variable. This was achieved by removing each of the replicate mesocosms and recalculating γ -pie for the remaining nine. The jackknifed γ -pie estimates were then used in the same two-factor linear model. All analyses were performed in R (version 3.1.2).

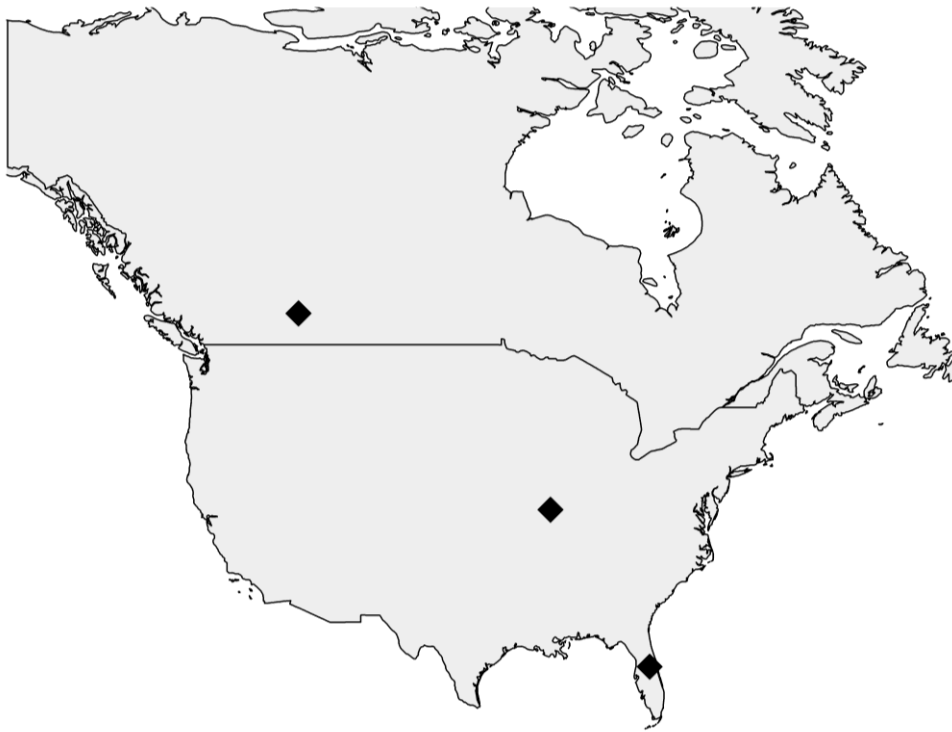


Figure 4.1. Map of experimental sites (◆). Sites correspond to latitudes of 28.5°N (Orlando, FL, USA), 38.5°N (St Louis, MO, USA), and 51.0°N (Calgary, AB, Canada).

4.3 Results

4.3.1 Initial Establishment

The best fit variance-covariance structure (lowest AIC) for aggregation of macrophyte communities in the control and extra initial biomass treatments across three years was unstructured (Table 4.1). This structure was used in the linear mixed model to test for the main effects of region, dispersal treatment, and year, as well as their interactions, on macrophyte aggregation using the `glht` function in the `multcomp`

package in R. Of the three main effects, region and dispersal treatment were significant (Table 4.2, Figures 4.2 - 4.3, $p < 0.05$). In addition, there was a significant interaction of region and dispersal treatment, indicating that the effect of initial biomass/propagule pressure varied across our three experimental sites (Table 4.2, $p < 0.05$). Post-hoc analyses were performed to investigate which regions differed in aggregation (Table 4.3). For the main effect of region, only the high- and mid-latitude sites differed significantly from each other (Figure 4.3, $p < 0.05$), with Calgary being significantly more aggregated than St. Louis. The lowest latitude site was marginally significantly different from the other two ($p < 0.10$, Table 4.3, Figure 4.3); Orlando was more aggregated than St. Louis and less aggregated than Calgary. Post hoc analyses were also performed to investigate how the initial dispersal treatment effect varied with region (Table 4.4). There was no significant treatment effect in our lowest latitude site, but the controls and extra initial biomass significantly differed in the two highest latitude sites (Table 4.4). The direction of the treatment effects was the same for both sites, with the extra initial biomass treatment having higher aggregation than the control tanks (Table 4.4, 4.8; Figure 4.4). There was also a marginally significant interaction between dispersal treatment and year (Table 4.2), though no a priori hypotheses warranted post hoc analyses on that interaction. The interaction plots of how macrophyte aggregation varied across regions and dispersal treatments over the three years is provided in Figure 4.5, showing that the two treatments reversed in effect in the low and mid-latitude sites. The rank abundance distributions of the ten most regionally abundant species for each region and each year are displayed in Figure 4.6 in order to visualize how γ -pie varied annually between the two treatments.

The best fit variance-covariance structure (lowest AIC) for aggregation of zooplankton communities in the control and extra initial biomass treatments across three years was an autoregressive structure (Table 4.5). This structure was used in the linear mixed model to test for the main effects of region, dispersal treatment, and year, as well as their interactions, on zooplankton aggregation. Of the three main effects, region was not significant (Figure 4.9) but year and dispersal treatment (Figure 4.7) were significant (Table 4.6, $p < 0.05$). In addition, all pairwise and the three-way interactions were significant (Table 4.6, $p < 0.05$). Post-hoc analyses were performed to further investigate the interaction between dispersal treatment and region (Table 4.7). As in the macrophyte communities, there was no significant treatment effect in our lowest latitude site, but there was a significant difference between the control and extra initial biomass treatments in the two highest latitude sites (Table 4.7; Figure 4.8). The direction of the treatment effects was the same for both sites, with the extra initial biomass treatment having lower aggregation than the control tanks (Figure 4.8, Table 4.8). We did not perform post-hoc analyses to further investigate the main and interaction effects with year due to a priori hypotheses. However, the interaction plots are shown in Figure 4.10 do reveal how zooplankton aggregation varied with dispersal treatment in each region over time. The rank abundance distributions of the ten most regionally abundant species for each region and each year are displayed in Figure 4.11 in order to visualize how γ -pie varied annually between the two treatments.

Macrophytes

Table 4.1. Comparison of variance-covariance structure of β -pie for macrophyte communities across three years.

	df	AIC	logLik
Compound	20	532.43	8.46
Unstructured	24	529.35	76.66
Autoregressive	20	531.98	28.13
Autoregressive Heterogeneous	22	595.33	6.16

Table 4.2. Linear mixed model for the effect of region, dispersal treatment (control versus extra initial biomass), and year on β -pie for macrophyte communities across three years.

	df	F-value	p-value
Region	2	11.1397	0.0001
Dispersal	1	4.6380	0.0358
Year	2	2.0907	0.1286
Region x Dispersal	2	3.3476	0.0426
Region x Year	4	1.5169	0.2024
Dispersal x Year	2	2.4337	0.0926
Region x Dispersal x Year	4	1.6687	0.1626

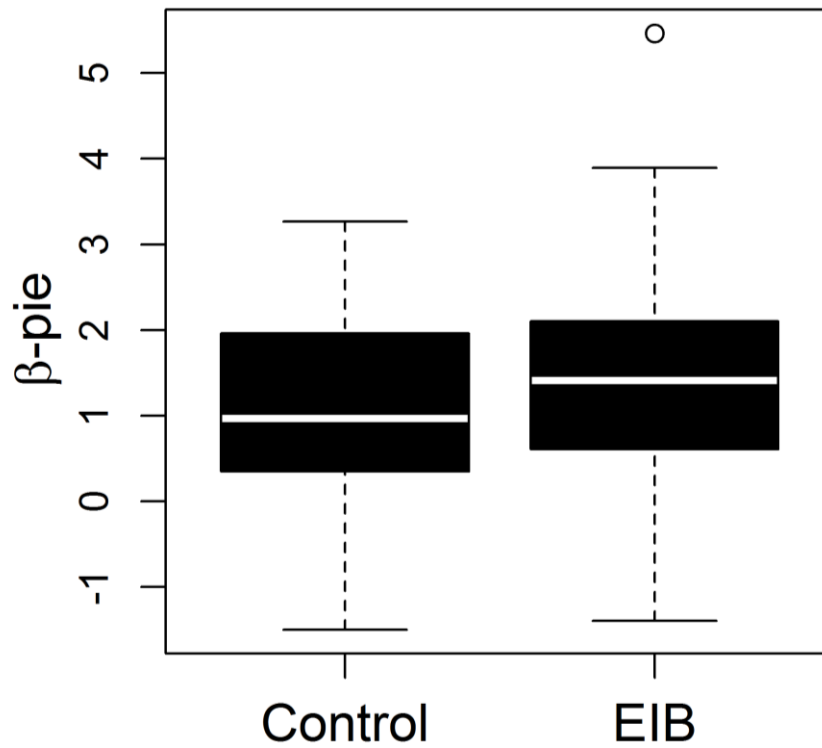


Figure 4.2. Macrophyte aggregation across the initial dispersal treatment (Control and extra initial biomass, EIB) from 2012-2014. Median values are in white.

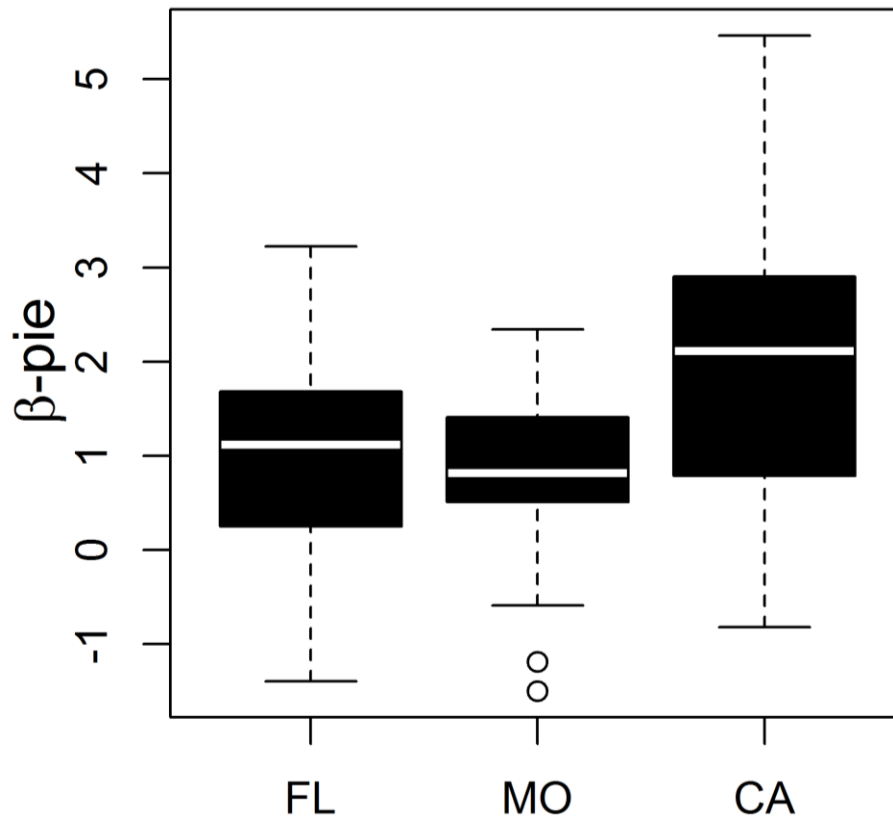


Figure 4.3. Macrophyte aggregation across each region (FL = Orlando, FL, USA; MO = St Louis, MO, USA; CA = Calgary, Alberta, Canada) in both the control and extra initial biomass treatments from 2012-2014. Median values are in white.

Table 4.3. Post-hoc contrasts for the main effect of region using Tukey's Honest Significance Difference.

	Estimate	z-value	p-value
MO - FL	-1.1783	-2.190	0.0728
FL - CA	-0.2756	-0.512	0.08654
MO - CA	-1.4539	-2.702	0.0189

Table 4.4. Post hoc contrasts of the dispersal treatment (control = ctrl vs. extra initial biomass = eib) on macrophyte aggregation within each region.

	Value	SE	t-value	p-value
FL eib – FL ctrl	-0.2499	0.2954	-0.8459	0.3988
MO eib – MO ctrl	0.6807	0.2989	2.2776	0.0240
CA eib – CA ctrl	0.7978	0.2954	2.7003	0.0076

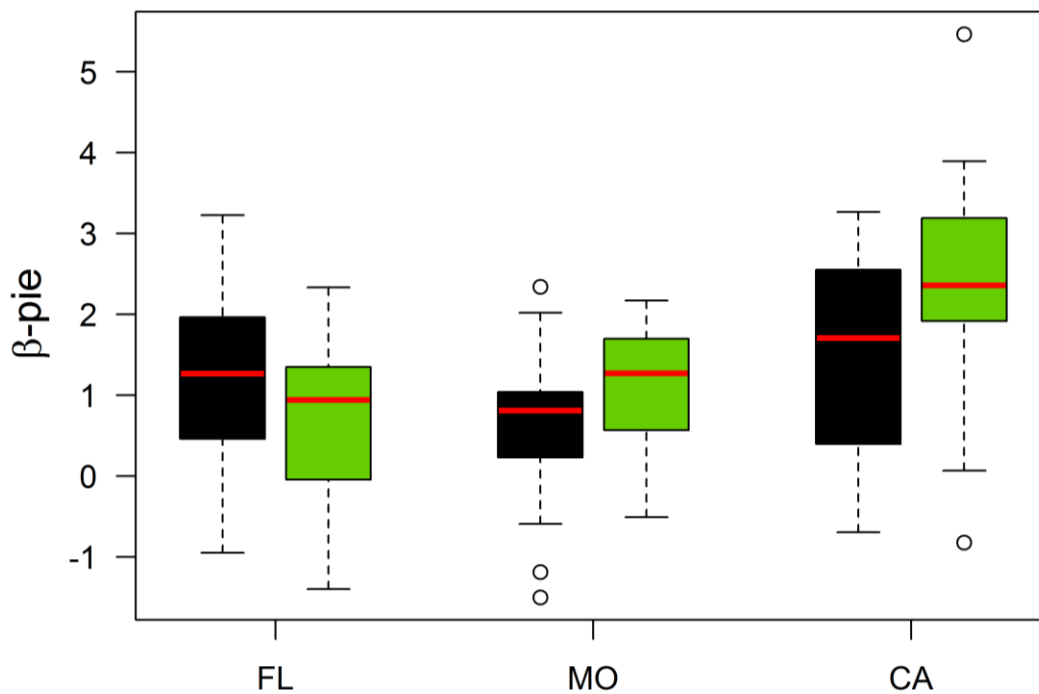


Figure 4.4. Macrophyte aggregation across each region (FL = Orlando, FL, USA; MO = St Louis, MO, USA; CA = Calgary, Alberta, Canada) and dispersal treatment (black = control, green = extra initial biomass) from 2012-2014. Median values are in red.

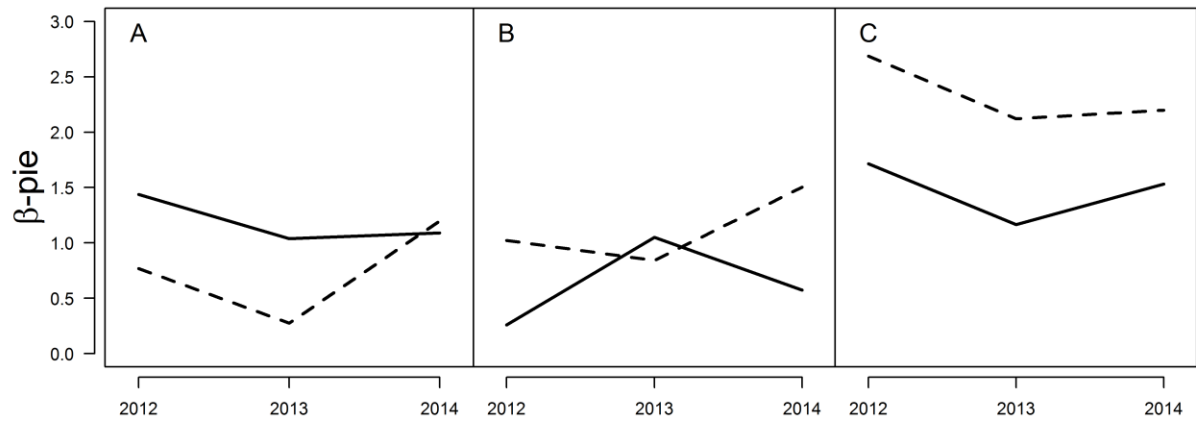


Figure 4.5. Interaction plots of the effect of the pre-assembly dispersal control (solid line) and extra biomass (dashed line) treatments on macrophyte aggregation ($\beta\text{-pie}$) across years for each experimental site: (A) Orlando, FL, USA; (B) St Louis, MO, USA; (C) Calgary, AB, CA.

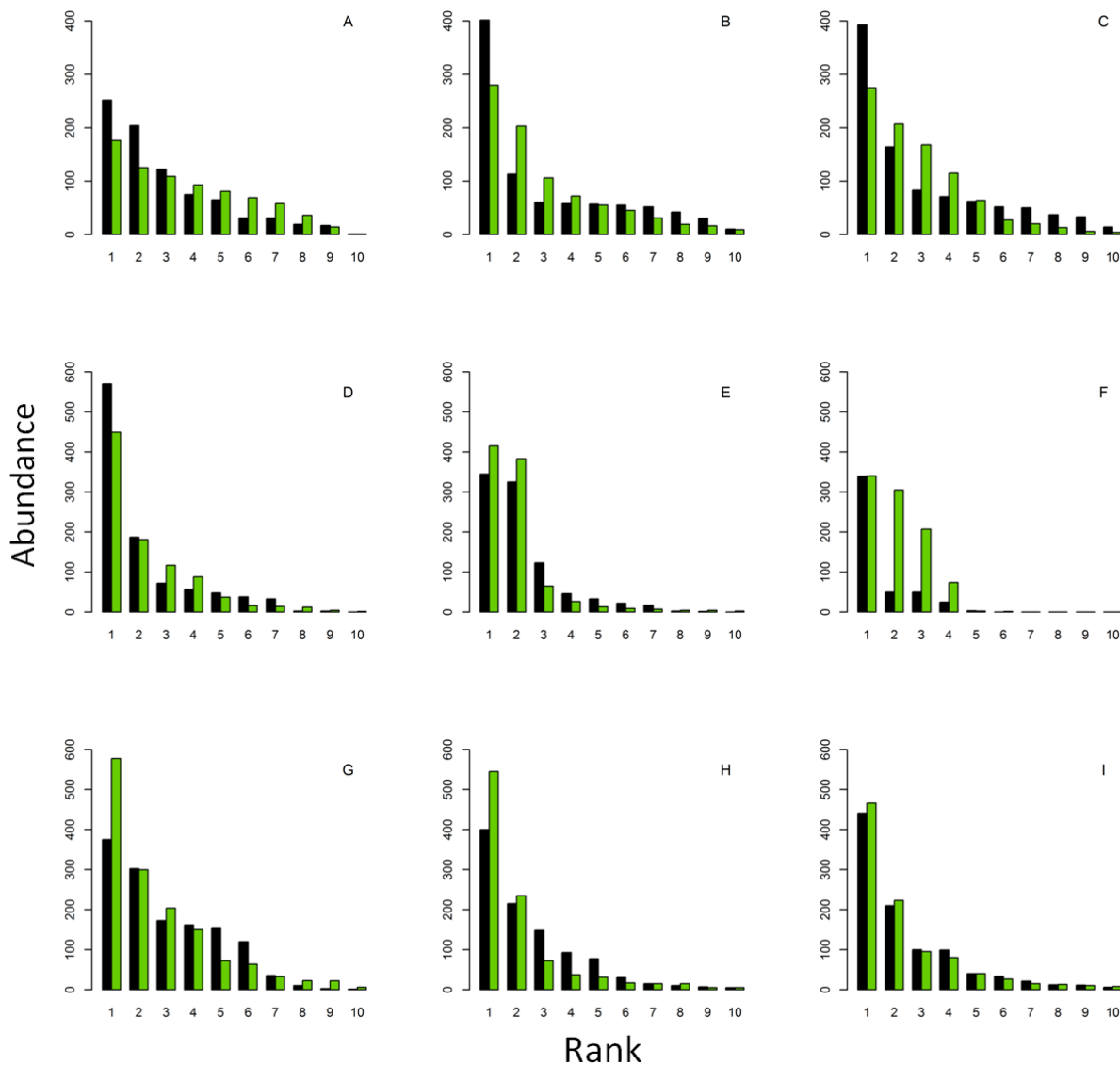


Figure 4.6. Regional rank percent cover distributions for the ten most abundant macrophyte species across three years in the control (black) and extra biomass (green) treatments. The top row (A, B, C) is Calgary, AB, Canada, the middle row (D, E, F) is St. Louis, MO, and the bottom row (G, H, I) is Orlando, FL. The years from 2012 – 2014 correspond to columns in order from left to right.

Zooplankton

Table 4.5. Comparison of variance-covariance structure of β -pie for zooplankton communities across three years.

	df	AIC	logLik
Compound	20	767.46	-363.73
Unstructured	24	768.22	-360.11
Autoregressive	20	763.64	-361.82
Autoregressive Heterogeneous	22	764.68	-360.34

Table 4.6. Linear mixed model for the effect of region, dispersal treatment (control versus extra initial biomass), and year on β -pie for zooplankton communities across three years.

	df	F-value	p-value
Region	2	2.0498	0.1387
Dispersal	1	14.9185	0.0003
Year	2	36.9117	< 0.0001
Region x Dispersal	2	3.5285	0.0363
Region x Year	4	31.8674	< 0.0001
Dispersal x Year	2	7.66593	0.0008
Region x Dispersal x Year	4	16.5117	< 0.0001

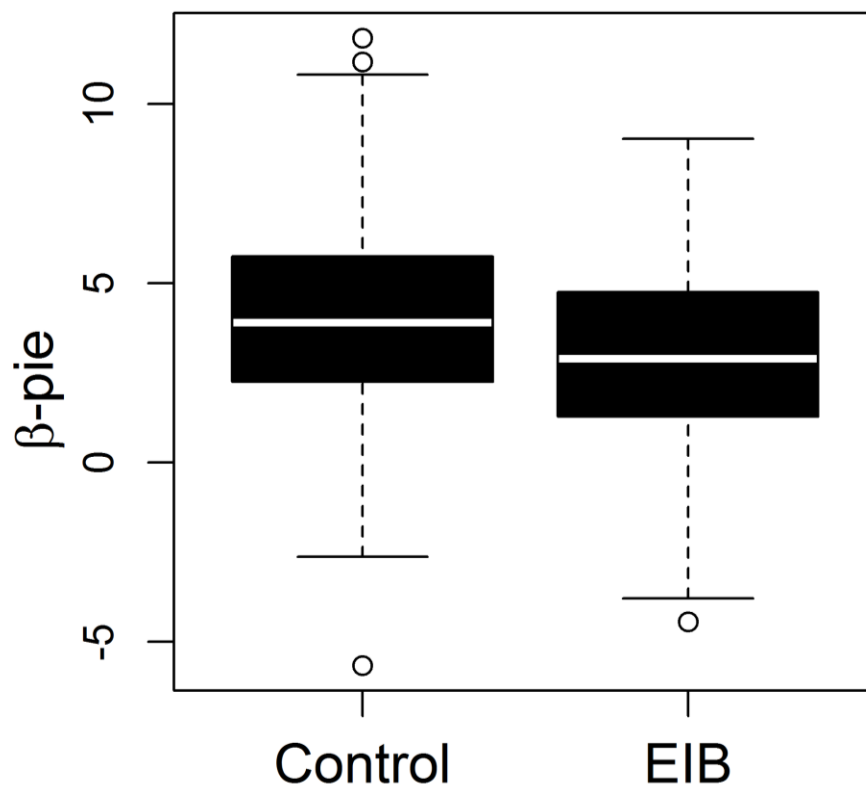


Figure 4.7. Zooplankton aggregation across the initial dispersal treatment (Control and extra initial biomass, EIB) from 2012-2014. Median values are in white. There was no significant difference in aggregation among treatments.

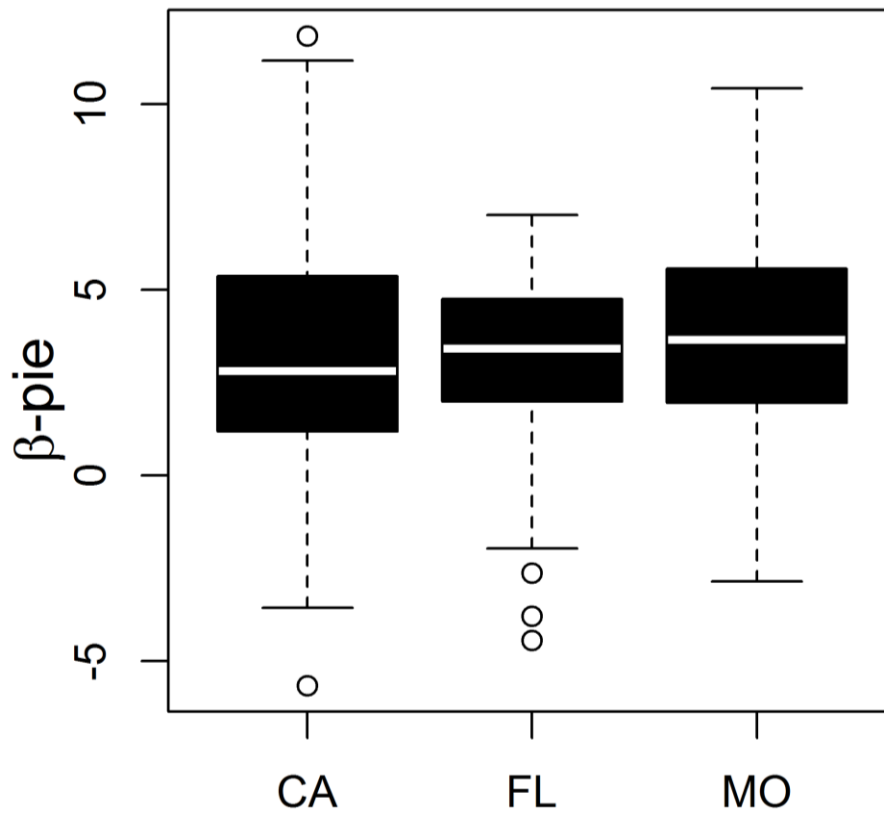


Figure 4.8. Zooplankton aggregation across each region (FL = Orlando, FL, USA; MO = St Louis, MO, USA; CA = Calgary, Alberta, Canada) in both the control and extra initial biomass treatments from 2012-2014. Median values are in white. There are no significant differences among regions.

Table 4.7. Post hoc contrasts for the dispersal treatment (control vs. extra initial biomass) on zooplankton aggregation within each region.

	Value	SE	t-value	p-value
FL eib – FL ctrl	0.4971	0.6244	0.7962	0.4270
MO eib – MO ctrl	-1.8354	0.6306	-2.9102	0.0041
CA eib – CA ctrl	-2.3387	0.6244	-3.7453	0.0002

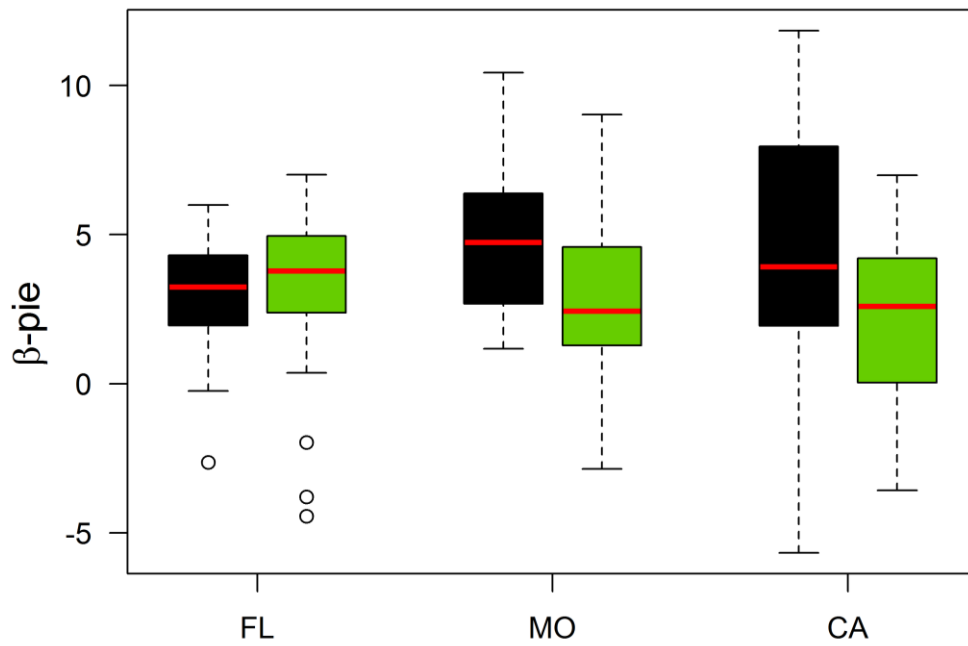


Figure 4.9. Zooplankton aggregation across region (FL = Orlando, FL, USA; MO = St Louis, MO, USA; CA = Calgary, Alberta, Canada) and dispersal treatment (black = control, green = extra initial biomass) from 2012-2014. Median values are in red.

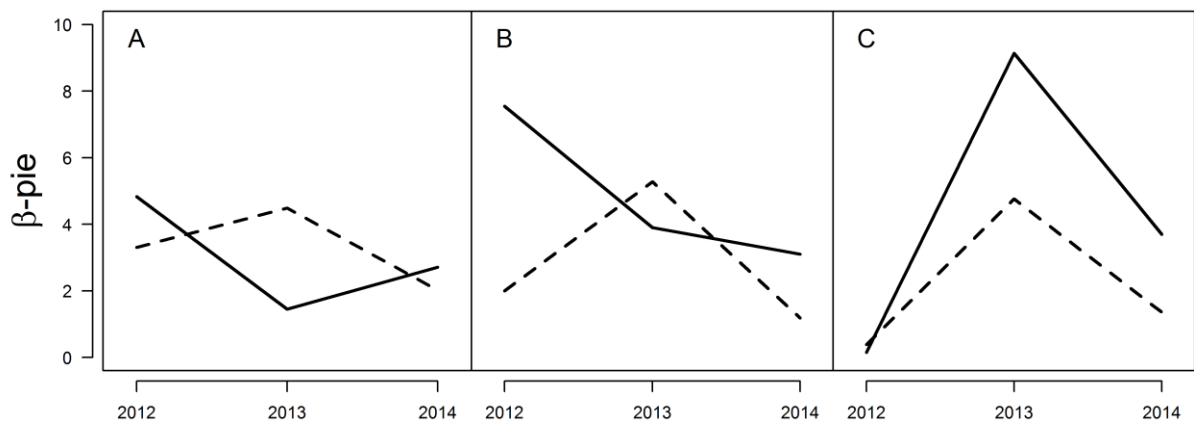


Figure 4.10. Interaction plots of the effect of the pre-assembly dispersal control (solid line) and extra biomass (dashed line) treatments on zooplankton aggregation (β -pie) across years for each experimental site: (A) Orlando, FL, USA; (B) St Louis, MO, USA; (C) Calgary, AB, CA.

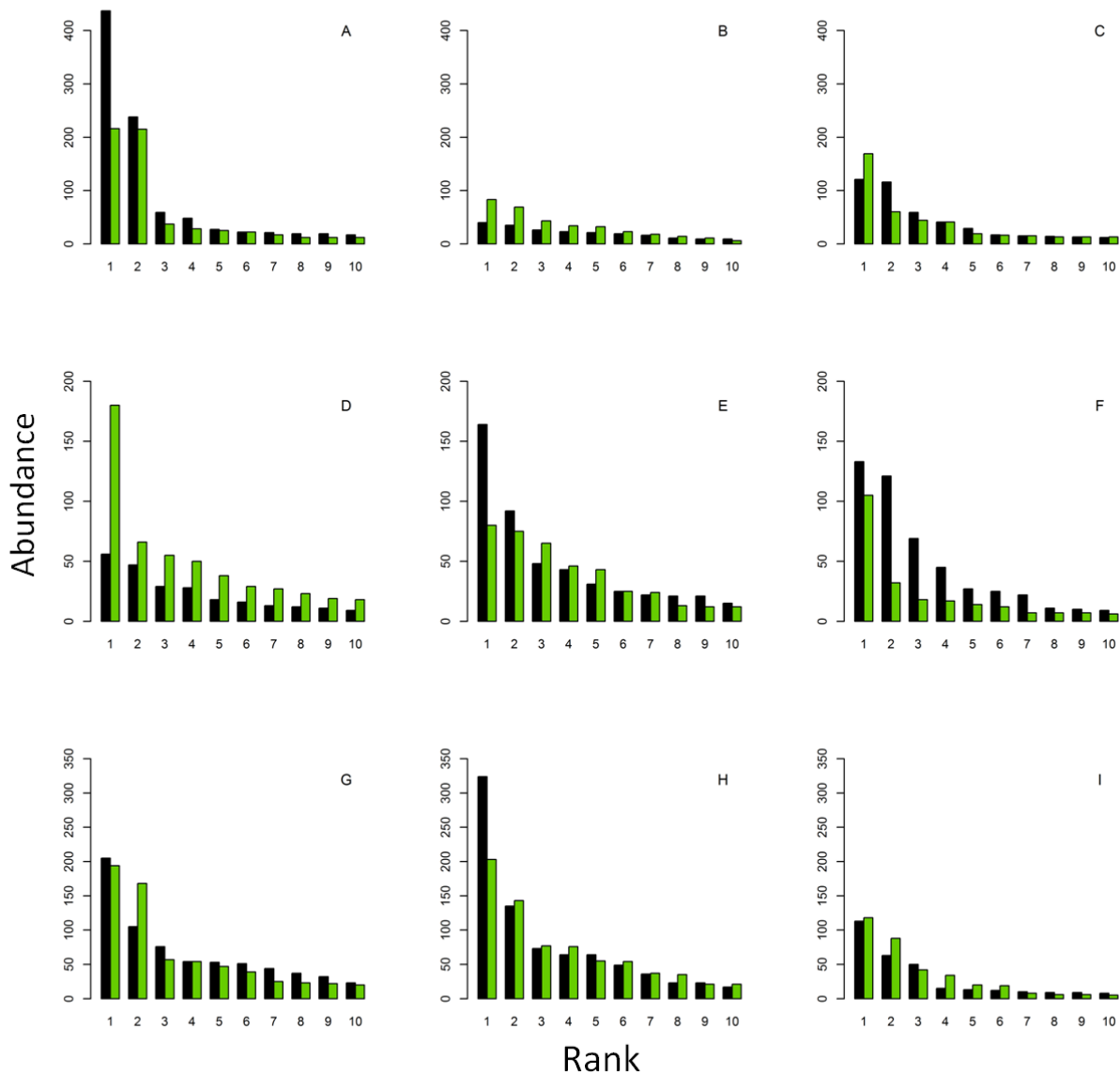


Figure 4.11. Regional rank abundance distributions for the ten most abundant zooplankton species across three years in the control (black) and extra biomass (green) treatments. The top row (A, B, C) is Calgary, AB, Canada, the middle row (D, E, F) is St. Louis, MO, and the bottom row (G, H, I) is Orlando, FL. The years from 2012 – 2014 correspond to columns in order from left to right.

Table 4.8. Effect size of the initial dispersal treatment on β -pie within each region (FL, MO, CA) for lentic macroinvertebrates and zooplankton from 2012-2014. Effect size is Cohen's d (margin of error of d).

	FL	MO	CA
Macroinvertebrates	0.229 (0.927)	-0.260 (0.957)	-0.077 (0.952)
Zooplankton	-0.11 (0.925)	0.622 (0.977)	0.429 (0.936)

4.3.2 Two Years Post Establishment

For the lentic macroinvertebrates, there was no effect of the late dispersal treatment on aggregation (Figure 4.12), but there was a significant main effect of region and a significant interaction between dispersal treatment and region ($p < 0.05$, Table 4.9). Post-hoc analyses on the main effect of region indicate that the mid-latitude site was significantly more aggregated than the other two sites, but that the low- and high-latitude sites were indistinguishable (Table 4.10, Figure 4.13, $p > 0.10$). Because there was a significant dispersal treatment by region interaction (Figure 4.14), we performed pairwise post-hoc contrasts on all treatment-region combinations using the Tukey's Honest Significance Difference method. In Table 4.11, we present only those contrasts of interest – within region dispersal treatment effects, and across region within treatment effects. Of those contrasts, only the control treatment of the mid-latitude site was significantly higher than the controls of the other two sites. Every other within region dispersal treatment effect and across region within dispersal treatment effect was non-significant ($p > 0.10$, Table 4.11).

For zooplankton communities, there was no effect of region on aggregation (Figure 4.15), but there was a significant dispersal treatment effect (Figure 4.16), as well

as a significant interaction between region and dispersal ($p < 0.05$, Table 4.12).

Because there was a significant interaction, we performed pairwise post-hoc contrasts on all treatment-region combinations using the Tukey's Honest Significance Difference method, though we only present the aforementioned planned contrasts in Table 4.13.

Within each region, there was a significant effect of the dispersal treatment on zooplankton aggregation, with the homogenization treatment having higher aggregation than the controls ($p > 0.05$, Figure 4.17, Table 4.13). The only other significant differences of the planned contrasts were between the homogenization treatments in the low- and mid-latitude sites, with the low-latitude homogenized tanks being significantly more aggregated than the mid-latitude homogenized tanks (Figure 4.17). Further, because the magnitude of the effect size for zooplankton tends to decrease with latitude, this suggests that the role of dispersal in community assembly may also decrease with latitude (Table 4.14).

As the expectation of homogenization is to decrease aggregation, which is contrary to the results of the zooplankton communities presented here, we further investigated what could be causing these increased aggregation in response to our dispersal treatment. Because aggregation is the difference between local and regional ENSpie values, we investigated if α -pie and/or γ -pie differed between these treatments (Table 4.15). We found that there was a significant treatment effect on α -pie, as well as a significant region by treatment interaction (Table 4.16). However, post-hoc analyses indicate that this is driven solely by the lowest-latitude site (Table 4.17). In contrast, there were significant effects of region, treatment, and their interaction on γ -pie (Table 4.18), and there were highly significant within region treatment effects at all three sites

(Table 4.19). To illustrate how zooplankton regional relative abundances varied for each region x treatment combination, we plotted the ten most abundant zooplankton species for each in pie charts (Figure 4.18).

Table 4.9. 2-way linear model for the effects of region, dispersal treatment, and their interaction for lentic macroinvertebrate aggregation. A) Sequential linear model using Type I sum of squares assessing the main effect of region before dispersal treatment. B) Sequential linear model using Type I sum of squares assessing the main effect of dispersal treatment before region.

A	df	SS	MS	F	p
Region	2	75.865	37.933	15.1054	< 0.0001
Dispersal Treatment	1	1.317	1.317	0.5245	0.4721
Region x Dispersal	2	16.013	8.007	3.1884	0.0493
Residuals	53	133.094	2.511		
B	df	SS	MS	F	p
Dispersal Treatment	1	1.821	1.821	0.7253	0.3982
Region	2	75.361	37.680	15.0050	< 0.0001
Region x Dispersal	2	16.013	8.007	3.1884	0.0493
Residuals	53	133.094	2.511		

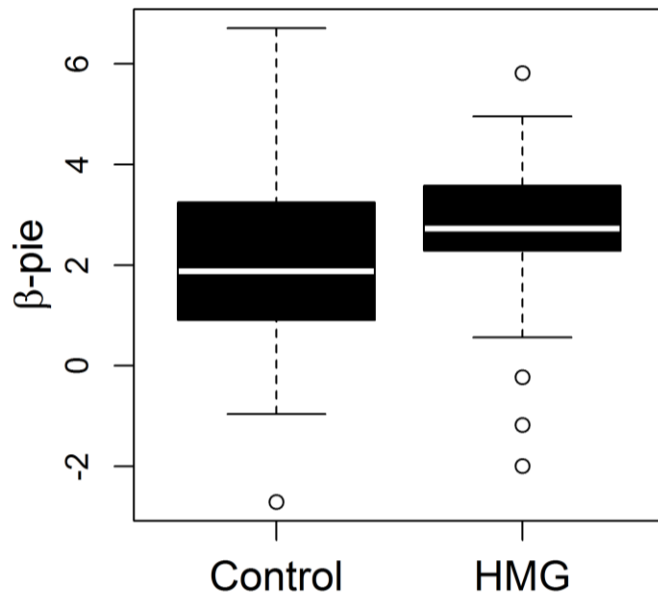


Figure 4.12. Lentic macroinvertebrate aggregation for the late dispersal treatment (Control and Homogenization, HMG). Median values are in white. There was no significant difference in aggregation among treatments.

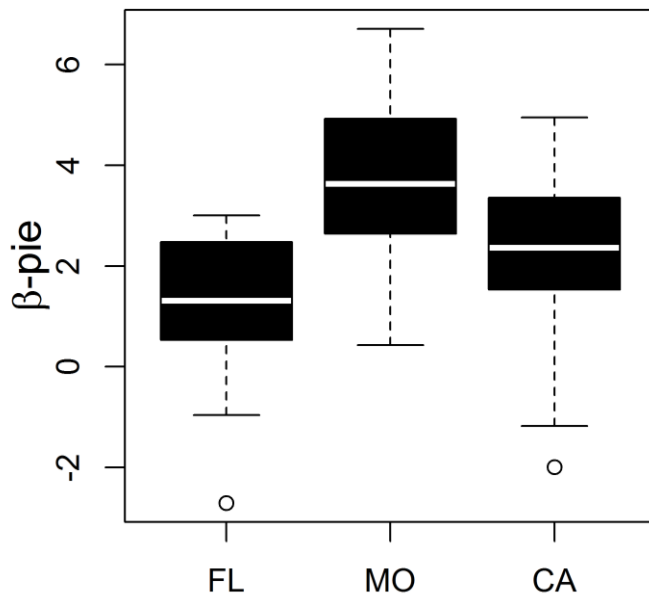


Figure 4.13. Lentic macroinvertebrate aggregation across each region (FL = Orlando, FL, USA; MO = St Louis, MO, USA; CA = Calgary, Alberta, Canada) in both the control and homogenization treatments from 2012-2014. Median values are in white.

Table 4.10. Post-hoc planned contrasts using Tukey's HSD for macroinvertebrate aggregation across regions (FL = Orlando, FL, USA; MO = St. Louis, MO, USA; CA = Calgary, Alberta, Canada).

Contrast	Diff	lwr	upr	p adj
FL - CA	-0.9069	-2.1152	0.3014	0.1762
MO – CA	1.8301	0.6139	3.0622	0.0019
MO - FL	2.7450	1.5208	3.9691	< 0.0001

Table 4.11. Post-hoc planned contrasts using Tukey's HSD for macroinvertebrate aggregation between the late dispersal treatments (hmg = homogenization; ctrl = control) within each region (FL = Orlando, FL, USA; MO = St. Louis, MO, USA; CA = Calgary, Alberta, Canada), and cross region effects within each dispersal treatment.

Contrast	Diff	lwr	upr	p adj
FL hmg - FL ctrl	1.7133	-0.3819	3.8085	0.1688
MO hmg – MO ctrl	-0.7354	-2.8881	1.4172	0.9126
CA hmg – CA ctrl	-0.1354	-2.2307	1.9598	1.0000
MO ctrl – FL ctrl	3.9886	1.8360	6.1413	< 0.0001
FL ctrl – CA ctrl	-1.8313	-3.9265	0.2640	0.1192
MO ctrl – CA ctrl	2.1574	0.0047	4.3100	0.0492
MO hmg – FL hmg	1.5400	-0.5553	3.6352	0.2675
FL hmg – CA hmg	0.0175	-2.0778	2.1127	1.0000
MO hmg – CA hmg	1.5574	-0.5378	3.6527	0.2561

Table 4.12. 2-way linear model for the effects of region, dispersal treatment, and their interaction for zooplankton aggregation. A) Sequential linear model using Type I sum of squares assessing the main effect of region before dispersal treatment. B) Sequential linear model using Type I sum of squares assessing the main effect of dispersal treatment before region.

A	df	SS	MS	F	p
Region	2	7.844	3.922	1.5583	0.2200
Dispersal Treatment	1	204.577	204.577	81.2784	< 0.0001
Region x Dispersal	2	25.084	12.542	4.9828	0.0104
Residuals	53	133.401	2.517		
B	df	SS	MS	F	p
Dispersal Treatment	1	202.719	202.179	180.5403	< 0.00001
Region	2	9.702	4.851	1.9273	0.1556
Region x Dispersal	2	25.084	12.542	4.9828	0.0104
Residuals	53	133.401	2.517		

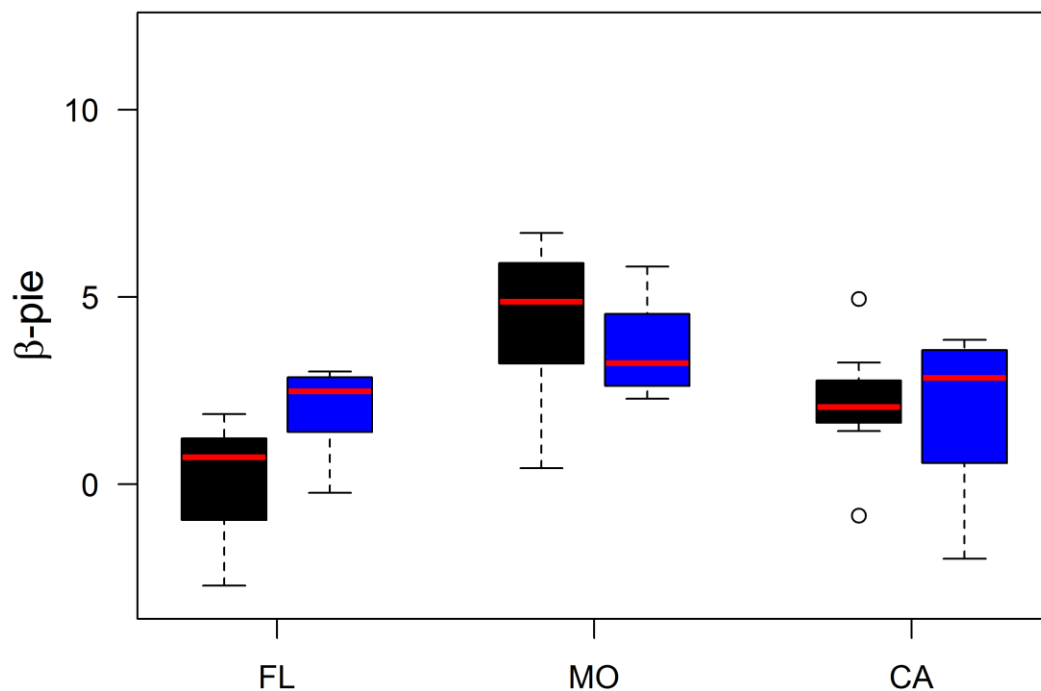


Figure 4.14. The effect of post-assembly dispersal treatment (black = control, blue = homogenization) on aggregation (β -pie) for lentic macroinvertebrates across each experimental site (FL = Orlando, FL, USA; MO = St. Louis, MO, USA; CA = Calgary, AB, CA). The red lines indicate median values.

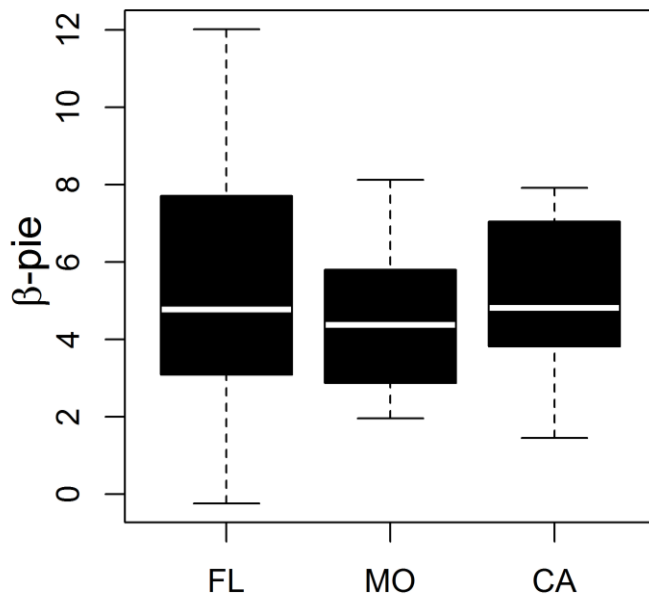


Figure 4.15. Zooplankton aggregation across each region (FL = Orlando, FL, USA; MO = St Louis, MO, USA; CA = Calgary, Alberta, Canada) from 2012-2014. Median values are in white.

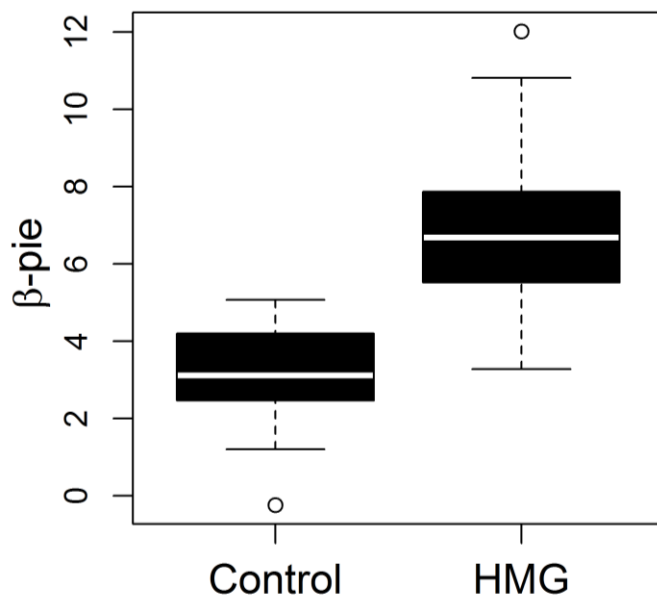


Figure 4.16. Zooplankton aggregation between for the late dispersal treatment (Control and Homogenization, HMG). Median values are in white.

Table 4.13. Post-hoc planned contrasts using Tukey's HSD for zooplankton aggregation between the late dispersal treatments (hmg=homogenization; ctrl=control) within each region (FL = Orlando, FL, USA; MO = St. Louis, MO, USA; CA = Calgary, AB, CA), and cross regional effects within each dispersal treatment.

Contrast	Diff	lwr	upr	p adj
FL hmng - FL ctrl	5.5454	3.4478	7.6431	< 0.0001
MO hmng – MO ctrl	2.8477	0.6926	5.0029	0.0035
CA hmng – CA ctrl	2.7382	0.6406	4.8359	0.0040
MO ctrl – FL ctrl	0.3769	-1.7782	2.5321	0.9953
FL ctrl – CA ctrl	-0.9863	-3.0839	1.1114	0.7327
MO ctrl – CA ctrl	-0.6094	-2.7645	1.5458	0.9594
MO hmng – FL hmng	-2.3207	-4.4184	-0.2231	0.0220
FL hmng – CA hmng	1.8209	-0.2767	3.9186	0.1239
MO hmng – CA hmng	-0.4998	-2.5975	1.5978	0.9806

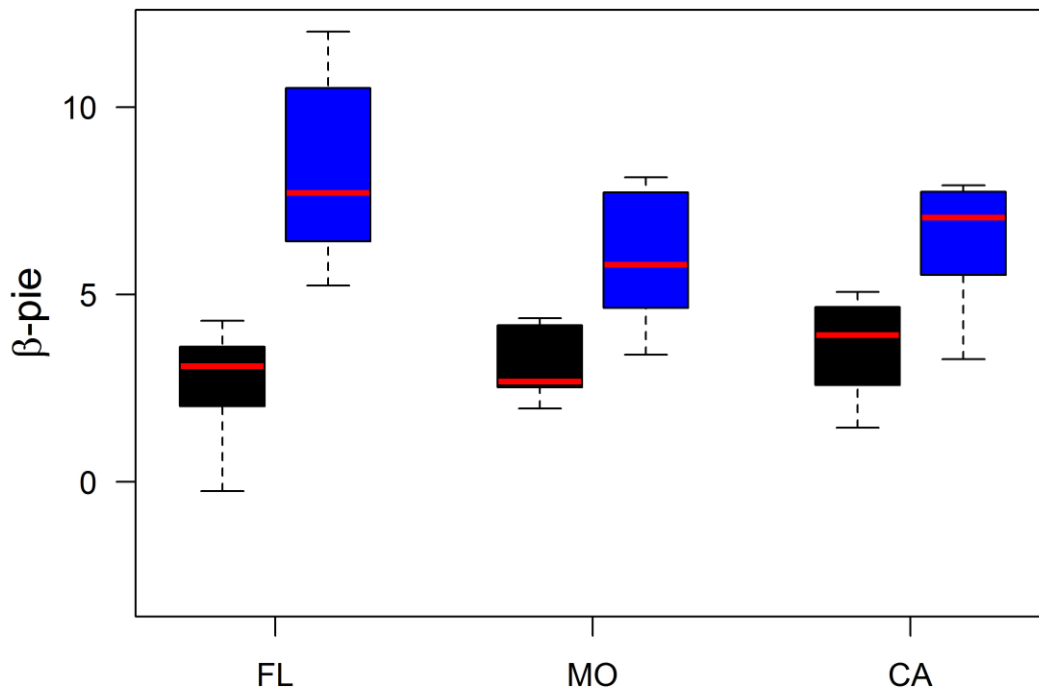


Figure 4.17. The effect of post-assembly dispersal treatment (black = control, blue = homogenization) on aggregation (β -pie) for zooplankton across each experimental site (FL = Orlando, FL, USA; MO = St. Louis, MO, USA; CA = Calgary, AB, CA). The red lines indicate median values.

Table 4.14. Effect size of the late dispersal treatment on β -pie within each region (FL, MO, CA) for lentic macroinvertebrates and zooplankton. Effect size is Cohen's d (margin of error of d).

	FL	MO	CA
Macroinvertebrates	-1.362 (1.036)	0.447 (0.965)	0.075 (0.924)
Zooplankton	-2.888 (1.357)	-2.130 (1.216)	-1.934 (1.139)

Table 4.15. Comparison of mean for α -, β -, and γ -pie for the zooplankton communities of the two dispersal treatments across each experimental site. No variance is reported for regional ENSpie as there is only one value per region-treatment combination.

	Control			Homogenization		
	α -pie	β -pie	γ -pie	α -pie	β -pie	γ -pie
FL	3.08 \pm 1.41	2.71 \pm 1.41	5.64 \pm 0.56	5.58 \pm 2.32	8.26 \pm 2.32	13.48 \pm 1.63
MO	3.67 \pm 0.95	3.09 \pm 0.95	6.66 \pm 0.54	4.39 \pm 1.64	5.94 \pm 1.64	10.17 \pm 0.87
CA	4.24 \pm 1.18	3.70 \pm 1.18	7.84 \pm 0.51	3.86 \pm 1.61	6.43 \pm 1.61	10.07 \pm 0.81

Table 4.16. 2-way linear model for the effects of region, dispersal treatment, and their interaction for zooplankton α -pie. A) Sequential linear model using Type I sum of squares assessing the main effect of region before dispersal treatment. B) Sequential linear model using Type I sum of squares assessing the main effect of dispersal treatment before region.

A	df	SS	MS	F	p
Region	2	1.03	0.517	0.205	0.8151
Dispersal Treatment	1	13.32	13.324	5.293	0.0254
Region x Dispersal	2	21.02	10.509	4.175	0.0207
Residuals	53	133.40	2.517		
B	df	SS	MS	F	p
Dispersal Treatment	1	13.23	13.225	5.254	0.0259
Region	2	1.13	0.566	0.225	0.7995
Region x Dispersal	2	21.02	10.509	4.175	0.0207
Residuals	53	133.4	2.517		

Table 4.17. Post-hoc planned contrasts using Tukey's HSD for zooplankton α -pie between the late dispersal treatments (hmg=homogenization; ctrl=control) within each region, and cross regional effects within each dispersal treatment.

Contrast	Diff	lwr	upr	p adj
FL hmng – FL ctrl	2.4981	0.4005	4.5958	0.0109
MO hmng – MO ctrl	0.7169	-1.4382	2.8721	0.9212
CA hmng – CA ctrl	-0.3748	-2.4725	1.7228	0.9948
MO ctrl – FL ctrl	0.5918	-1.5634	2.7469	0.9641
FL ctrl – CA ctrl	-1.1574	-3.2550	0.9403	0.5821
MO ctrl – CA ctrl	-0.5656	-2.7207	1.5895	0.9704
MO hmng – FL hmng	-1.1895	-3.2871	0.9082	0.5530
FL hmng – CA hmng	1.7156	-0.3820	3.8133	0.1687
MO hmng – CA hmng	0.5262	-1.5715	2.6239	0.9757

Table 4.18. 2-way linear model for the effects of region, dispersal treatment, and their interaction for the jackknifed estimate of zooplankton γ -pie. A) Sequential linear model using Type I sum of squares assessing the main effect of region before dispersal treatment. B) Sequential linear model using Type I sum of squares assessing the main effect of dispersal treatment before region.

A	df	SS	MS	F	p
Region	2	11.01	5.506	6.626	0.0027
Dispersal Treatment	1	304.29	304.294	366.152	< 0.0001
Region x Dispersal	2	86.20	43.101	51.862	< 0.0001
Residuals	53	44.05	0.831		
B	df	SS	MS	F	p
Dispersal Treatment	1	301.79	301.79	363.139	<0.0001
Region	2	13.52	6.758	8.132	0.0008
Region x Dispersal	2	86.20	43.101	51.862	<0.0001
Residuals	53	44.05	0.831		

Table 4.19. Post-hoc planned contrasts using Tukey's HSD for the jackknifed estimate of zooplankton γ -pie between the late dispersal treatments (hmg=homogenization; ctrl=control) within each region, and cross regional effects within each dispersal treatment.

Contrast	Diff	lwr	upr	p adj
FL hmng – FL ctrl	7.8394	6.6341	9.0448	<0.0001
MO hmng – MO ctrl	3.5121	2.2737	4.7504	<0.0001
CA hmng – CA ctrl	2.2264	1.0210	3.4317	<0.0001
MO ctrl – FL ctrl	1.0134	-0.2250	2.2517	0.1682
FL ctrl – CA ctrl	2.2008	0.9955	3.4061	<0.0001
MO ctrl – CA ctrl	1.1874	-0.0509	2.4258	0.0673
MO hmng – FL hmng	-3.3140	-4.5193	-2.1087	<0.0001
FL hmng – CA hmng	-3.4123	-4.6176	-2.2069	<0.0001
MO hmng – CA hmng	-0.0983	-1.3036	1.1071	0.9999

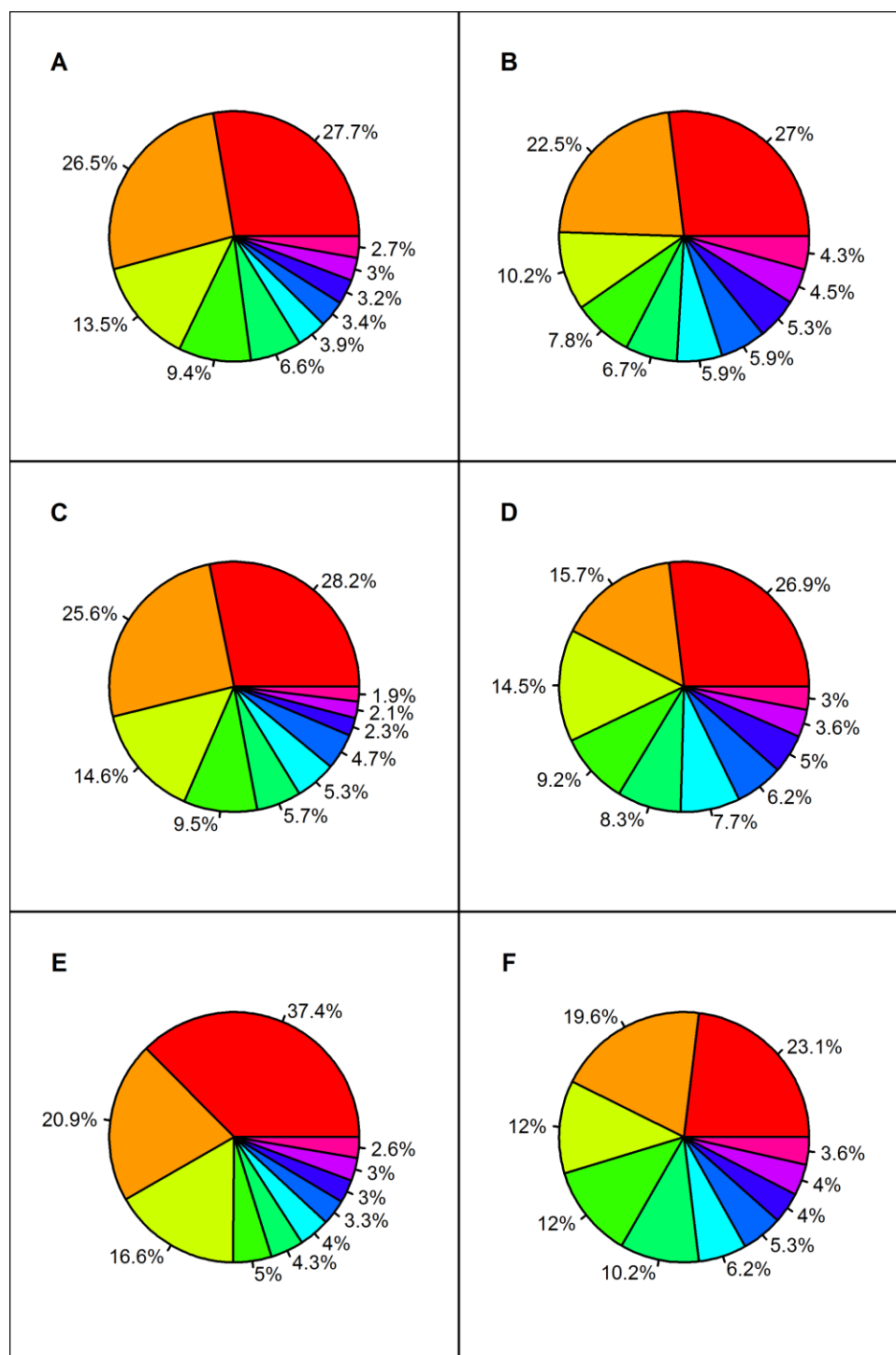


Figure 4.18. Pie charts showing the relative abundances in percents of the ten most abundant species of zooplankton in the control (left panel) and homogenization (right panel) treatments. The rows descend in latitude, with the top (A,B) being Calgary, AB, CA; the middle (C,D) is St. Louis, MO, USA; and the bottom (E,F) is Orlando, FL, USA.

4.4 Discussion

The effect of dispersal treatment either early or late in assembly varied with taxonomic group. Our general expectation was that dispersal should tend to homogenize communities, thus decreasing aggregation. Interestingly, however, increased initial propagule pressure resulted in significantly increasing (macrophytes) or decreasing (zooplankton) aggregation. There were also no general trends in aggregation with region, although there were many significant initial dispersal treatment by regional effects. Similarly, for the post-assembly dispersal treatment, we did not find an overall effect of decreased aggregation. In fact, the treatment was only significant for zooplankton, wherein aggregation actually increased. There was a also significant regional effect, but this did not consistently change with latitude. Like initial dispersal, the post assembly dispersal treatment did often depend on region, which together emphasize that the effect dispersal depends on regional differences in abiotic and biotic filtering, as well as the importance of stochasticity in regulating community composition.

4.4.1 Initial Establishment

Propagule pressure in the early stages of community assembly had varying effects on each of the manipulated taxonomic groups. For the macrophytes, extra initial biomass actually increased aggregation relative to the controls (Figure 4.2). However, the opposite happened with respect to zooplankton aggregation (Figure

4.7). One major difference between these groups is the way in which we manipulated initial propagule pressure. Many zooplankton species (rotifers and cladocerans, as well as some copepods) commonly form dormant resting stages that settle in the benthos. Because we added 5x the volume of zooplankton collected from the water column of nearby ponds, as well as 10x the volume of benthic sediment (presumably with many dormant species) to the extra biomass treatment, we can be fairly confident that initial propagule pressure of zooplankton differed between the dispersal treatments. Although macrophytes also have seed banks that may have been present in the added benthic sediments, our main way of manipulating macrophyte biomass was with live individuals, which was only 3-5 times higher in the extra biomass treatment relative to the controls. Since we rarely encountered macrophyte species that were not added as live individuals in the mesocosms, it would indicate that benthic sediments likely contributed little to macrophyte communities. Therefore, the zooplankton communities likely got a much stronger dispersal treatment effect relative to the macrophytes. Nevertheless, this would not explain the opposite treatment effects on aggregation for these two groups.

The effect of region/latitude also varied with taxonomic group. The macrophytes had significantly lower aggregation in the mid-latitude site than in the highest latitude site, with the low latitude site being marginally different from the other two (Figure 4.3). In contrast, there was no significant main effect of region for zooplankton aggregation (Figure 4.9). These inconsistent treatment and regional effects may simply be driven by varying species pools among each region. Each region contained many unique species, with only a few overlapping species of either macrophytes or zooplankton in

multiple sites. Furthermore, the treatment effect for macrophytes is mainly driven by the highest latitude site, with the other two sites having inconsistent initial dispersal treatment effects from one year to the next (Figure 4.5). One factor driving these regional differences may be due to varying environmental conditions across years and across regions. For example, the summer of 2013 was a severe drought period throughout much of the United States, and water had to be added to the two most southern sites that year to keep the mesocosms from drying out. Thus, these unexpected treatment and regional effects may result from the way in which macrophytes and zooplankton responded to drought, or other environmental differences, differentially across North America.

For both taxonomic groups, there was a significant interaction between region and initial dispersal treatment. This resulted from a significant initial dispersal treatment effect within the mid- and high-latitude sites, but not at the lowest latitude site (Tables 4.4, 4.7). That is, there were no differences in aggregation in Florida communities for either taxonomic group in the control and extra initial biomass treatments. In contrast, there were significant differences in aggregation between the two dispersal treatments at the mid- and high-latitude sites. This is of note because it indicates that in some regions, possibly relating to latitude, initial propagule pressure does not matter when it comes to community assembly. One explanation could be that lower latitude communities may effectively be assembling over a longer period of time due to less severe seasonal differences there. In contrast, the two high latitude sites were frozen, or partially frozen, for several months each year. Thus, it could be that with increased active assembly time, differences in initial propagule pressure matter

less. In other words, over time alternative states eventually converge, similar to the decades-old idea of ecological succession (Cowles 1899, Clements 1936). It is also of note that as we go from the low-high latitude sites, the differences between treatments get larger (Table 4.8), which would also be consistent with the idea that active assembly time tends to decrease the effect of initial propagule pressure.

Another way to interpret these results is in considering how species interactions during the initial phases of community assembly ultimately affect community composition. In this context, the extra initial biomass treatment increased the probability that species interactions during early colonization, as opposed to purely stochastic assembly, could affect aggregation patterns. With this perspective, when species at the two higher latitude sites were given a greater opportunity to interact during colonization, it affected aggregation for both macrophyte and zooplankton communities. In contrast, the initial dispersal treatment at the low latitude site had no effect on community composition. Due to this lack of treatment effect in Florida, these results would be consistent with the idea that the low latitude regional pool effectively had more ecologically equivalent, or neutral species, compared to the high latitude pools. However, we acknowledge that this is not a direct test of the degree of species' neutrality for entire species pools.

The final result of note in this first experiment is that the extra initial biomass treatment of macrophytes showed higher aggregation relative to controls in the high latitude sites, which is the opposite pattern for zooplankton communities. One explanation for this result is that when given greater opportunity for initial macrophyte colonists to interact, it resulted in more alternative states. Although this is more difficult

to interpret, it could simply result from the differences in how we manipulated initial biomass in the two groups. Perhaps the low propagule pressure treatment (controls) of both macrophytes and zooplankton resulted in communities dominated by a few of superior colonizers and thus low aggregation. When propagule pressure of macrophytes was moderately increased in the extra initial biomass treatment, it resulted in the manifestation of a completion-colonization tradeoff (Levins and Culver 1971), where the inferior colonizers but superior competitors could establish themselves in some mesocosms and the superior colonizers in others. In contrast, because the extra biomass treatment for zooplankton was likely much stronger than for macrophytes, it might have ensured that only the best zooplankton competitors were established in each extra initial biomass mesocosm, thus decreasing zooplankton aggregation relative to the controls. In other words, the zooplankton extra biomass treatment ensured that the dominant competitors established in all communities at the high latitude sites (lower aggregation), while the more moderate treatment for the macrophytes simply gave a chance for both the good colonists and the good competitors to establish (higher aggregation).

4.4.2 Two Years Post Establishment

The effect of dispersal later in community assembly also varied with taxonomic group and strength of the dispersal treatment. When dispersal was high (lentic macroinvertebrates), there was no difference between the control and homogenization treatments, although there was significant region effect and interaction between the

dispersal treatment and region (Table 4.9). With respect to the main effect of region, the mid-latitude site was significantly more aggregated than the high- and low-latitude sites. This is not consistent with aggregation varying consistently with latitude and suggests that other regional influences are of greater importance. Interestingly, when examining the post-hoc planned contrasts of all treatment differences within each region, and all regional differences within treatment, the only differences were cross-regional within treatment. More specifically, of all 9 contrasts, only the mid-latitude control aggregation was significantly higher than both the low- and high-latitude control treatments. Again, this indicates that some factor(s) at the Missouri site created higher aggregation. Although the dispersal treatment was fairly high at 50% of each community, it should be noted that all species included in this experiment were active dispersers, mainly Coleoptera, Odonata, and Hemiptera. In fact, the dominant lentic invertebrates were the larval odonates which must leave the aquatic community in order to reach their aerial adult stages. This means that any larvae found in a given year was the result of an aerial adult laying eggs in that tank during their active reproduction stage. Therefore, it is not very surprising that such high levels of dispersal in the homogenization treatment did not have an effect on aggregation patterns.

The lower homogenization treatment, consisting of removing and homogenizing just five percent of the zooplankton communities, resulted in very different aggregation patterns. There was no main effect of region (Figure 4.15), but a significant effect of dispersal treatment and its interaction with region (Figures 4.16, 4.17). Most surprisingly, the homogenization treatment led to higher rather than lower aggregation

relative to controls (Figure 4.16, Table 4.14) across all three regions. Dispersal increasing aggregation was an unexpected result. A commonly discussed mechanism to explain how dispersal can result in greater aggregation is if species are sorting along environmental gradients (Leibold et al. 2004). However, because we attempted to minimize any abiotic differences by using mesocosms, it seems unlikely that is the major factor creating aggregation in this experiment. Another explanation is that zooplankton species are sorting with respect to *biotic* heterogeneity. Each community received small amounts of macrophyte, zooplankton, and other invertebrate inocula, which resulted in some degree of aggregation during community assembly. The mesocosms were also open to active dispersers, which further created heterogeneous communities based on differences in biotic environments. Because zooplankton are not active dispersers, there were likely relatively few opportunities for zooplankton communities to reach these differing biotic communities. However, after the homogenization treatment, zooplankton had the opportunity to better match their biotic (and likely biotically influenced abiotic) environment.

The other significant pairwise differences beside among treatments within regions, was that the homogenization treatment at the low latitude site was significantly larger than the two higher latitude sites. There were no cross-regional differences with respect to controls. In contrast to the results from the initial dispersal treatment, homogenization resulted in more highly aggregated communities in Florida relative to the higher latitude sites. Although much more experimentation on this would be needed, these results together suggest low latitude zooplankton behave more neutral in early stages of assembly, but more deterministic as assembly progresses.

Because the homogenization results for zooplankton were fairly unexpected, we further explored which (or both) scales (local versus regional) influenced aggregation. To achieve this we ran the same linear models and post-hoc contrasts for α -pie (Tables 4.16-4.17). Of the two main effects, only the dispersal treatment was significant, as was the interaction between dispersal and region. Of all nine planned contrasts, the only significant difference was between the homogenization and control treatments at the low-latitude site, which clearly cannot account for significant treatment effects on aggregation for all three sites. Instead, it seems likely that much of the variation in aggregation in response to the late dispersal treatment is driven by differences in the regional SAD (Tables 4.18-4.19, Figure 4.18). As is evident in Figure 4.18, the homogenization treatment has more even relative species abundances than the controls. We therefore conclude that although both regional and local scales affect aggregation, at least in this experiment, it seems that regional level processes have a greater impact on aggregation.

As has long been known, these experiments reiterate that dispersal affects community assembly and composition patterns (Chase 2003, Levine and Murrell 2003, Stachowicz and Tilman 2005). However, what is less well understood is how the timing of dispersal events affect aggregation and how that might vary among regions/latitudes and functional or taxonomic groups (Chase and Myers 2011). As was the case in Florida, here we have shown that initial propagule pressure, and thus initial species interactions, might not matter when it comes to aggregation patterns. Additionally, its importance may vary with latitude as was the trend for both macrophytes and zooplankton. However, this could simply from longer effective

assembly time as latitude (and freezing temperatures) decreases. Either explanation would still be notable, though, as it is often believed that initial differences in dispersal events can play a large role in regulating community composition (Weiher and Keddy 1999, Körner et al. 2008). Here, we show that over time it might not matter very much, or that its importance actually varies with region/latitude. In contrast, dispersal later in assembly has quite different effects. With dispersal-limited groups (zooplankton), our dispersal treatment after 2 years of assembly actually increased aggregation, and this effect was significantly larger in the lowest latitude site. Although we initially attempted to eliminate abiotic differences among mesocosms, it became evident that as the biotic communities diverged, it also affected several abiotic factors that were measured (e.g. water temperature, pH, primary productivity). This experiment thus emphasizes the role of species interactions and species sorting along biotic factors, which, in comparison to abiotic factors, is far less investigated in community assembly research (Kraft et al. 2015).

4.5 References

- Cadotte, M. W. 2006. Dispersal and Species Diversity: A Meta Analysis. *The American Naturalist* **167**:913-924.
- Chase, J. M. 2003. Community assembly: when should history matter? *Oecologia* **136**:489-498.
- Chase, J. M. and T. M. Knight. 2013. Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters* **16**:17-26.
- Chase, J. M. and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **366**:2351-2363.
- Clements, F. E. C. F. p. d. F. 1936. Nature and Structure of the Climax. *Journal of Ecology* **24**:252-284.
- Cowles, H. C. C. F. p. d. F. 1899. The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan. Part I.-Geographical Relations of the Dune Floras. *Botanical Gazette* **27**:95-117.
- Dauby, G. and O. J. Hardy. 2012. Sampled-based estimation of diversity sensu stricto by transforming Hurlbert diversities into effective number of species. *Ecography* **35**:661-672.
- Fukami, T. and M. Nakajima. 2011. Community assembly: alternative stable states or alternative transient states? *Ecology Letters* **14**:973-984.

- Gómez-Rodríguez, C., A. Freijeiro, and A. Baselga. 2015. Dispersal and ecological traits explain differences in beta diversity patterns of European beetles. *Journal of Biogeography* **42**:1526-1537.
- Holt, R. D. and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* **149**:745-764.
- Hubbell, S. P. 2006. Neutral theory and the evolution of ecological equivalence. *Ecology* **87**:1387-1398.
- Hurlbert, S.H., 1971, The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, v. 52, p. 577-586. (On explicit calculation of rarefaction richness and derivation of Hurlbert's PIE measure of evenness.)
- Jost, L. 2006. Entropy and diversity. *Oikos* **113**:363-375.
- Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* **29**:592-599.
- Lande, R. S., B. Engen, and B. E. Saether. 2003. Stochastic population dynamics in ecology and conservation. . Oxford University Press, Oxford.
- Law, R. and R. D. Morton. 1993. Alternative permanent states of ecological communities. *Ecology* **74**:1347-1361.
- Law, R. and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* **77**:762-775.
- Lee, S. C. and J. F. Bruno. 2009. Propagule supply controls grazer community structure and primary production in a benthic marine ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* **106**:7052-7057.

- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**:601-613.
- Levine, J. M. and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology Evolution and Systematics* **34**:549-574.
- Levins, R. and D. Culver. 1971. Regional coexistence of species and competition between rare species (mathematical model/habitable patches). *Proceedings of the National Academy of Sciences of the United States of America* **68**:1246-&.
- Logue, J. B., N. Mouquet, H. Peter, H. Hillebrand, and G. Metacommunity Working. 2011. Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution* **26**:482-491.
- Mouquet, N. and M. Loreau. 2002. Coexistence in metacommunities: The regional similarity hypothesis. *American Naturalist* **159**:420-426.
- Mouquet, N. and M. Loreau. 2003. Community patterns in source-sink metacommunities. *American Naturalist* **162**:544-557.
- Myers, J. A., J. M. Chase, I. Jimenez, P. M. Jorgensen, A. Araujo-Murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters* **16**:151-157.
- Myers, J. A. and K. E. Harms. 2009. Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* **92**:676-686.

- Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* **104**:377-387.
- Orrock, J. L. and R. J. Fletcher. 2005. Changes in community size affect the outcome of competition. *American Naturalist* **166**:107-111.
- Qian, H. 2009. Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography* **18**:327-332.
- Qian, H. and R. E. Ricklefs. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography* **21**:341-351.
- Questad, E. J. and B. L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters* **11**:717-726.
- Scheiner, S. M. and J. Gurevitch. 2001. *Design and Analysis of Ecological Experiments*. Oxford University Press, Oxford.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is There a Latitudinal Gradient in the Importance of Biotic Interactions? *Annual Review of Ecology, Evolution, and Systematics* **40**:245-269.
- Stachowicz, J. J. and D. Tilman. 2005. Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. .in D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. *Species Invasions: Insights Into Ecology, Evolution, and Biogeography*. Sinauer Associates, Inc., Massachusetts.

- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**:81-92.
- Vanschoenwinkel, B., F. Buschke, and L. Brendonck. 2013. Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. *Ecology* **94**:2547-2557.
- Vellend, M., D. S. Srivastava, K. M. Anderson, C. D. Brown, J. E. Jankowski, E. J. Kleynhans, N. J. B. Kraft, A. D. Letaw, A. A. M. Macdonald, J. E. Maclean, I. H. Myers-Smith, A. R. Norris, and X. X. Xue. 2014. Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos* **123**:1420-1430.
- Wallace, A. R. 1878. *Tropical Nature and Other Essays*. Macmillan, New York.
- Wang, Z., J. Fang, Z. Tang, and L. Shi. 2012. Geographical patterns in the beta diversity of China's woody plants: the influence of space, environment and range size. *Ecography* **35**:1092-1102.

Chapter 5: Conclusion

This dissertation combined observational data with experiments to document and understand how and why β -diversity patterns in pond communities change across latitudes in North America. A major notable approach used throughout this research is the way in which we quantified β -diversity - the additive difference between the regional and local scale values of Hurlbert's probability of interspecific encounter as an effective number of species, or β -pie. Although this is not a particularly new metric (see Olszewski 2004), it is not commonly used in β -diversity research, which is noteworthy because β -pie reduces some of the numerical dependencies between α -, β -, and γ -diversity.

The way that many researchers currently attempt to account for such sampling effects is through a variety of null models that hold constant different aspects of local communities and/or regional species pools (Chase et al. 2011, e.g. Kraft et al. 2011, Stegen et al. 2013, Qian and Wang 2015). However, as mentioned throughout this dissertation, recent research is increasingly showing that null models do not always (and likely cannot) account for all numerical sampling effects on β -diversity (e.g. Mori et al. 2015, Xu et al. 2015, Tucker et al. 2016). In fact, there are two particular sampling effects that β -pie, without employing null models, handles very well – the number of individuals in a local community and the size/shape of the regional species pools (Chase and Knight 2013). By using β -pie in this dissertation, we have therefore avoided some of the sampling effects that have caused much contention in community ecology and β -diversity research in recent years.

Indeed, the observational research collected in the second chapter, showed that despite the fact that we found a latitudinal gradient in species richness, there was not a consistent significant trend in β -pie in space or time. In fact, we found a positive trend for spatial β -pie in the first year, a negative trend the next year, and then no trend in the third year. We also failed to find a link between spatial and temporal β -pie, which is increasing found in other research (Adler et al. 2005) and has led to the adoption of the acronym STAR for the species time area relationship. This first chapter thus introduces an alternative, non-pairwise way to quantify β -diversity, as well as emphasizing that the presence or absence of β -diversity trends along environmental or biogeographic gradients can fluctuate through time.

Because β -diversity arises due to various community assembly processes acting and interacting simultaneously in nature, in the third and fourth chapters we focused on specific assembly processes using large outdoor mesocosm experiments replicated at three latitudes in North America. For the third chapter we applied a strong environmental filter, drought, to assess its effect on spatial β -pie and if this effect varied consistently with latitude. Interestingly, the main effect of drought was actually to increase β -pie relative to the controls. This was fairly unexpected as a similar experiment performed several years previously found the opposite effect, the interpretation of which was that only a subset of species are drought-tolerant, leading to greater regional homogenization (Chase 2007). However, as we found the opposite pattern, one interpretation is that environmental filters can allow some regionally rare species to increase in abundance, for example if they disproportionately affect regionally abundant species.

The experiment also analyzed β -pie for two different groups of species separately – active and passive dispersers. The results varied substantially among dispersal groups and drought had inconsistent effects across the three latitudes. The passive dispersers slightly decreased in aggregation at the lowest latitude site, the opposite effect was found at the mid-latitude site, and there was no effect in the high-latitude site. In contrast there was a large increase in aggregation in response to drought for the passive dispersers at the low-latitude site, with no effect observed in the other two sites. Such results suggest that the exact same environmental filter imposed at similar times can have really variable effects that depend on regional differences (including species pools) and that there is no clear, consistent pattern in how filters interact with dispersal limitation.

Because β -pie is the difference between α -pie and γ -pie, we also examined the effect of drought on those values. Surprisingly, α -pie was only affected by drought for the active dispersers in one site. However, there were large effects of drought on γ -pie, with the direction of change in β -pie being matched by the same directional effect on γ -pie. That is, diversity in local communities was generally not affected by this filter, but drought did greatly affect regional diversity by increasing intraspecific aggregation among local communities.

The final chapter focuses on the role of dispersal in affecting aggregation at two different stages of assembly – initial establishment and two years after initial assembly. For both experiments there were two levels of dispersal – high and low – with the general expectation that higher dispersal will tend to homogenize communities, thus decreasing aggregation. However, in both experiments we saw that increased dispersal

varied in its effect on aggregation depending on taxonomic group and region. One result of note however, is that across all regions the higher dispersal treatment caused an increase in aggregation for zooplankton communities, with much smaller and varying effects for lentic macroinvertebrates. A major difference between these two groups is their dispersal ability, with the former being passive and the latter mostly active dispersers. Thus, this result could indicate that experimentally induced dispersal only matters when species are dispersal limited, and the effect of increased aggregation suggests that such a dispersal treatment allows for greater species sorting along biotic or abiotic gradients, even in fairly abiotically homogeneous environments.

Through observational and experimental work, this dissertation makes several conclusions about the state of community assembly research. First, the concept of β -diversity is still in flux, as is the appropriate way to quantify it without conflating sampling effects. Indeed, it seems the field is fairly disjunct when it comes to methods and interpretation of β -diversity variation, and it would benefit community ecology to make raw datasets accessible for large-scale analyses across systems and biogeographic analysis, enabling the comparisons of different metrics and/or null models. To this end, I will place all of the data from this experiment up on github for open access.

Both the observational work and experimental work emphasize the dynamic nature of communities and the need for more long term data with an array of taxonomic groups with different dispersal abilities. Although there has been a concerted effort to gather long term data for tree communities across the globe, these same types of network are needed for shorter lived organisms and active dispersers that might

respond to environmental variation and other of community assembly much more rapidly.

Lastly, the experiments in particular emphasized the many ways in which, even in somewhat controlled environments, the interplay between dispersal, species interactions, environmental filtering, and stochasticity can yield incredibly variable outcomes for β -diversity. Such results suggest the need for much more attention be paid to, both theoretically and empirically, the ways in which different assembly mechanisms interact in order for community assembly research to move forward.

5.1 References

- Adler, P. B., E. P. White, W. K. Lauenroth, D. M. Kaufman, A. Rassweiler, and J. A. Rusak. 2005. Evidence for a general species-time-area relationship. *Ecology* **86**:2032-2039.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* **104**:17430-17434.
- Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. C. a. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere* **2**:1-11.
- Chase, J. M. and T. M. Knight. 2013. Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters* **16**:17-26.
- Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science* **333**:1755-1758.
- Mori, A. S., S. Fujii, R. Kitagawa, and D. Koide. 2015. Null model approaches to evaluating the relative role of different assembly processes in shaping ecological communities. *Oecologia* **178**:261-273.

- Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* **104**:377-387.
- Qian, H. and X. L. Wang. 2015. Global relationships between beta diversity and latitude after accounting for regional diversity. *Ecological Informatics* **25**:10-13.
- Stegen, J. C., A. L. Freestone, T. O. Crist, M. J. Anderson, J. M. Chase, L. S. Comita, H. V. Cornell, K. F. Davies, S. P. Harrison, A. H. Hurlbert, B. D. Inouye, N. J. B. Kraft, J. A. Myers, N. J. Sanders, N. G. Swenson, and M. Vellend. 2013. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. *Global Ecology and Biogeography* **22**:202-212.
- Tucker, C. M., L. G. Shoemaker, K. F. Davies, D. R. Nemergut, and B. A. Melbourne. 2016. Differentiating between niche and neutral assembly in metacommunities using null models of beta-diversity. *Oikos* **125**:778-789.
- Xu, W. B., G. K. Chen, C. R. Liu, and K. P. Ma. 2015. Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Global Ecology and Biogeography* **24**:1170-1180.